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Species Diversity at Wet Tropical Environment I. Polymorphic Variation and Population Structure of *Schismatoglottis lancifolia* (Araceae) in West Sumatra

Mitsuru HOTTA, Hiroshi OKADA and Motomi ITO

ABSTRACT *Schismatoglottis lancifolia* (Araceae) is a forest floor herb in tropical rain forest and a native of Sumatra. It shows a typical outcross pollination and protogyny, i.e., the male flowers supply pollen grains one day after the female matures. The pollinator is some Diptera and/or small beetles and the pollen flow seems to be restricted in small area. The reproduction is carried out mainly by seeds with a few exception of vegetative propagation.

The population of *S. lancifolia* preserves several polymorphic characters in not only phenotype but also karyotype, e.g., the color of beneath of the leaf, presence or absence of leaf surface mottle, type of satellite chromosome, and the number of B-chromosome. We analyze the polymorphic variations in these characters at different populations to clarify the population structure and the infra-species diversity.

Sixty-one sites in 13 locations, including four plots for forest ecological survey were studied. The spatial position of individuals at these plots, Gajabuih, Pinang Pinang, Pinang Pinang Atas and Airsirah, are recorded on the maps for further analysis, and put together into clones judged from spatial arrangement, karyotype and leaf characters.

The $\overset{*}{m}$-m methods are applied for the analysis of the spatial distribution patterns of both individuals and clones. The results indicate the existence of double clump structure in populations; smaller clump is calculated to be of about 1 m^2, while larger the one is of about 100 m^2 which is looser than the former. By these analyses the hierarchy of population structure is clarified as; micro-, breeding-, topo- and local-population.

Variation patterns of characters in locations (almost the same as topo-populations) are classified into two types. One is that the ratio of each character fluctuates location by location. Leaf beneath color and B-chromosome show this pattern. The other pattern is that the ratio of each character takes rather constant value irrespective of location. Leaf mottle and satellite chromosome display this pattern.

The correlation between some environmental gradients and ratios of the characters are analyzed. None of the characters are associated with environmental gradient, but the possibility that the polymorphism is maintained by different selection direction under different microhabitat is still a matter of debate.

KEY WORDS *Schismatoglottis lancifolia* / Araceae / polymorphism / population structure / reproductive biology / cytotaxonomy / satellite chromosome / B-chromosome / speciation / tropics / diversity

Contents

Introduction

Recent advancement in biosystematics offers some proposed models for the speciation of plants in temperate zone (Grant, 1981). While the evidences for the complexity of the structure of tropical ecosystem and the explosive diversity of species in tropical zone have accumulated, but data for clarification of the speciation phenomena are still few.

In 1969 van Steenis said that "The difference in speciation between tropical rain forest compared with the flora of the temperate zone is largely one of the degree, not of principle, the tropics offering a low survival value, with less competition intensity, less correlation with ecological niches, a high species density, with more isolated species and many more 'taxonomic terata',...." He concluded that saltatory evolution is easily caused in tropical region. Fedorov (1966) suggested that low population density of species and asynchronous blooming in tropical rain forests induce frequent occurrence of inbreeding which causes hindrance of gene flow, resulting in accelerated speciation. Against this opinion, based on wide field observation and experiences in Malesian tropical rain forest, Ashton (1969) concluded that the main factor in speciation is ecological and geographical isolation. Morawetz (1982) investigated infra- and interspecific variation of *Jacaranda* (Bignoniaceae) at neotropics and discussed speciation from the view point of ecological segregations.

These contradictory ideas originate from comparatively insufficient store of her-

barium specimens, and lack of experiment and field experiences in tropics. Here we aim to improve the disadvantageous issue in tropical zone by providing abundant informations from our field survey. In the first step of the analytical study of the complexity and diversity of the species in tropical region it is necessary to elucidate the situations in tropics, such as population structure, pattern of polymorphism in local populations, its genetical base and the ecological characters of species.

Theoretically the basic unit of evolution is population in which gene recombination occurs freely by sexual reproduction (Fisher, 1930). Many computer simulations and farm experiments on the population structure and breeding size have been reported (Handel, 1983). Nevertheless, the actual population size and structure in field is still obscure, especially in the humid tropics where there is extreme richness of species as well as a very large number of closely related species. To understand the extraordinary richness and variabilities of tropic biota, we must analyze the population structure and variations in typical sexual reproductive species. It may be the first step of evolutionary research on biota of the tropical environments.

In this paper we report both phenotypic and karyotypic polymorphisms and population structure of *Schismatoglottis lancifolia* Hall. f. et Engler (Araceae) in tropical rain forests in West Sumatra. This species has typical sexual reproduction, enormous variation, both phenotypic and karyotypic, and commonly distributed in the forest floor of the study area. Since cultivation of this species by cutting the stem is very easily successful under humid and high temperature conditions, therefore we chose as a representative this pretty aroid for the analysis of population diversity. A part of the data until 1983 was previously reported (Hotta et al., 1984a).

ACKNOWLEDGMENTS This study is a portion of reports in the Sumatra Nature Study project, a joint field research program cooperate Andalas University of Indonesia and Kyoto University of Japan. We wish to thank all members of the project, specially Drs. Mawardi Yunus, Dr. Amsir Bakar, Drs. Rustam Usman of Andalas University and Dr. S. Kawamura of Kyoto University for their encouragement. We are also indebted to Dr. Setijati Sastrapradja, Dr. Mien A. Rifai, Dr. Kuswata Kartawinata, Dr. Soedarsono Riswan of Lembaga Biologi Nasional, Bogor, Indonesia, kindly helped our study. We are grateful to two gardeners, Mr. Asril (Andalas University) and Mr. H. Nishimura (Kyoto University) who carefully cultivated the plants for cytological study. Our thanks are also extended to many others who helped this work, particularly Drs. Rusjdi Tamin, MSc. Syahbuddin, MSc. Marlis Rahman, Drs. Erizal Muktahr, Mrs. Lusi Bebasari, Dr. K. Ogino, Dr. K. Yoneda, Dr. T. Wakatsuki and Dr. T. Kohyama. The field work was supported by a Grant-in-Aid to overseas scientific survey from the Ministry of Education, Science and Culture, Japan (1980, 35643052; 1982, 57041029; 1984, 59041037), and financed by the JSPS (1981), and the Kajima Foundation (1983).

I. General Description of the Area and Materials

1. Environment of the Study Area

Mt. (Gunong) Gadut, the study area, is located in Barisan range some 20 km east of Padang city, the provincial capital of West Sumatra. The altitude is 1859 m above sea level, and the steep and big Ulu Gadut valley cuts the southwestern slope of the mountain. These mountain ranges are very effective in catching the rains brought by wind from Indian Ocean, and this area has far wetter climate than that of other region

in Sumatra. The climatological data of the selected places are given in Table 1. The precipitation at Padang is exceedingly higher than that of other places, reaching nearly 5000 mm per annum. At Indarung, near the mouth of Ulu Gadut valley, it reaches nearly 6000 mm, which continues constantly throughout a year. Though we do not have the climate record of Ulu Gadut valley, our short experience shows that Ulu Gadut valley has heavier rainfall than Indarung, reaching 7000 mm or more per annum, which is one of the highest rainfall in humid tropics. The climate of Padang area has a seasonal variation ranging from extreme rainfall from September to December, to the dry period from January to March and June to August (Table 1). The seasonal variation is not so remarkable but induces seasonal rhythm in vegetation.

Table 1. Mean monthly precipitation (mm) of selected places in Sumatra

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Ann
Medan	137	91	104	132	175	132	135	178	211	259	246	229	2029
Bukittingi	224	163	212	246	173	124	90	148	176	229	221	243	2249
Padang	361	252	355	409	340	289	250	350	459	573	581	545	4764
Indarung	499	368	480	521	450	349	293	425	536	656	715	622	5914

Areas below 600 m altitude in Ulu Gadut valley is covered with Foothill Dipterocarp forest, characterized by many fagaceous members (*Lithocarpus*, *Quercus* and *Castanopsis*). They are dominant tree member in second layer of this forest. Hill Dipterocarp forest, Hill Oak forest and Montane Oak forest occur on altitudes of 600 m to 1000 m, 1000 m to 1500 m and above, respectively (Ogino et al., 1984).

2. *Schismatoglottis lancifolia*, Features and Habitat

The excess humidity and the well preserved vegetation give Ulu Gadut valley the richest aroid flora in West Sumatra. There are numerous aroid species in the Mt. Gadut area (Hotta, 1984b).

The genus *Schismatoglottis*, a perennial ground aroid, occurs mainly in moist forest floor of Malesian tropics (ca. 70 spp.), and only 1 or 2 species in South America. Undoubtedly West Malesia (Sumatra, Malaya and Borneo) is the main center of species diversity of this genus. Our study area has the richest flora of this genus in Sumatra island; 6 species has been identified in Mt. Gadut area, viz. *S. batoensis* Engler, *S. calyptrata* (Roxb.) Zoll. et Mor., *S. lancifolia* Hall. f. et Engler (=*S. kurimana* v. Ard. v. Rosen.), *S. rupestris* Zoll. et Mor., *S. treubii* Engler, and *S. okadai*, a new species. On one hand these species vary considerably in their morphological characters and ecological habitat. On the other hand, they show uniformity in their cytological characteristics, such as chromosome number, all of them being diploid with $2n=26$ (except a few triploid clones of *S. lancifolia*, Okada, 1984a). In the genus *Schismatoglottis* two closely related species, *S. lancifolia* and *S. okadai*, have distinct and segregated ecological and topographical habitat. The former occurs usually in dense forest floors or rocky places of ridges and upper slopes of hills, while the latter (*S. okadai*) occurs only in limited and specialized habitats in or near rapid flowing streams (three localities in Mt. Gadut area). These two species form a closely related and undoubtedly natural

group by similarities in their floral and karyological characters (both species express nearly the same numerical variations of B-chromosome, see Hotta et al., 1984a. Details will appear in another paper of this series).

Schismatoglottis lancifolia was first described by Engler in 1912 based on his observation on a cultivated clone in the Botanic Garden of Buitenzorg (Bogor). According to the note of Engler, this clone was "collected from Borneo (?) by J. G. Hallier". The type specimen in the Herbarium Bogoriense is in a very poor condition, sterile and only two small lanceolate leaves attached in a sheet, but they have irregular white mottles on the leaf surface. By the leaf shapes, texture and pattern of its white mottle, this species undoubtedly is the same to *S. kurimana* v. Ard. v. Rosen. which was described in 1922 from West Sumatra (Sg. Kuriman). In 1893, Hallier visited West Coast of Sumatra (near Padang) and might had a chance to collect living material of this species. Around Padang city, *S. lancifolia* grows mainly in areas ranging from mid-slope to high ridge, lowland and Hill Dipterocarp forests and lower part of Hill Oak forests, but never invades into wet or heavily humid places. The upper limit of distribution range is restricted to mountainous zones (ca. 1000–1200 meters altitude). Undoubtedly this upper limit of altitudinal distribution is decided by the temperature. In the forests at ca. 1100 meters altitude sometimes temperature may reach to less than 15°C.

Field observations of habitat segregation show that *Schismatoglottis lancifolia* occupies a special and distinct habitat separated from other species of the genus, and usually does not form mixed population with other species of *Schismatoglottis*. It is well known that in biological species, isolation is an important factor in the independence of species (pointed out by many authors, cf. Grant, 1981), and usually each biological species has specialized habitat or niche. Morphologically, *S. lancifolia* shows wide variation in leaf characters, but is a good biological species with distinct ecological and topographical habitat among the species of *Schismatoglottis* that exist in Mt. Gadut area.

3. Sites of Material Collection

For the analysis of morphological and karyological characters, fresh stem cuttings from 2374 individuals were collected and cultivated in Ulu Gadut campus, Andalas University, in 1982 and 1984. The above specimens were gathered from 59 sites at 12 locations in Mt. Gadut area (Limau Manis, Gn. Gadut, Ulu Gadut, Setia Mulia and Airsirah), central West Sumatra, and 2 sites of Bondjor area (Lurah Berangin), northern West Sumatra. The details of the localities and sites with the observed chromosome numbers of individuals and short ecological notes are summarized in Table 2 and Figure 1. These sites include four permanent plots for study of forest ecology, i.e. Gajabuih, Pinang Pinang, Pinang Pinang Atas, and Airsirah. Short descriptions of these permanent plots are as follows;

Gajabuih plot—This plot is situated on the northwestern slope near a ridge descending from Bt. Gajabuih (760 m in altitude), a hill top on a ridge of Mt. Gadut. This plot was established in December 1980. The original vegetation type is multi-stratal Foothill Dipterocarp forest with emergent tree of *Shorea* spp. and *Swintonia schwenkii* (T. et B.) T. et B. ex Hook. f. The plot area had been partly disturbed by villagers' logging.

Table 2. Localities and sites of study area. Number collected (Coll. no.), number of individual observed karyotype (Chro. ob.), and ecological notes and altitude of each location.

Location	Samp. ar. (m^2)	Coll. no.	Chro. ob.	Ecol. notes, alt.
LIMAU MANIS AREA				
<Limau Manis>				
LM –1	10*	20	12	River side cliff, under low-
–2	10*	16	11	land forest, ca. 290 m.
GN. GADUT AND RIDGE OF BT. KAMBUT AREA				
<Bali Bukit>				
BA –1	10	6	5	Under foothill forest, on
–2	50	20	10	ridge, ca. 600 m.
<Bt. Batu Bajolang>				
BB –1	10	10	7	Secondary forest or foothill
–2	10	11	9	forests, on ridge, ca. 550–
–3	10	11	7	650 m.
–4	10	11	9	
–5	10	8	1	
–6	10	16	7	
–7	10	10	3	
<Bt. Lantik>				
BC –1	5	4	4	Under foothill forest, on
2	10	26	20	ridge, ca. 600–650 m.
3	5	12	10	On slope, ca. 550 m.
<Bt. Kambut>				
KA –1	10	4	2	Under hill forest, ca. 900 m.
2	100	15	8	On slope, ca. 750 m.
3	100	28	2	Foothill forest, ca. 550 m.
KB	10	6	4	Under hill forest, ca. 950 m.
KC	5	3	1	On ridge, ca. 1050 m.
KD	10*	18	7	On slope. ca. 1000 m.
PH –1	10*	14	2	Under hill forest,
–2	10*	12	1	ridge, ca. 800–900 m.
–3	5*	12	3	
<Gn. Gadut>				
GG –1	15	11	8	Under hill forest, ca. 1100 m.
–2	5*	7	7	ca. 1050 m.
ULU GADUT AREA				
<Pinang Pinang>				
PP –1	11500	805	138	Under foothill forest,
–1'	4500	308	–	slope to ridge, ca. 500–600 m.
–2	2000	72	67	
–3	100	27	17	
–4	10(×3)	27	26	
<Gajabuih>				
GJ –1	10000	456	343	Under foothill forest, slope
–2	30	24	20	to ridge, ca. 600–650 m.
–3	10	8	8	ca. 550 m.
–4	5(×3)*	51	23	ca. 700 m.
–5	50*	26	3	ca. 700 m.
<Bt. Gambir>				
GM –1	10(×2)*	15	5	Under foothill forest, slope,

(cont'd.)

(Table 2. cont'd)

Location	Samp. ar. (m^2)	Coll. no.	Chro. ob.	Ecol. notes, alt.
–2	50*	28	3	ca. 600–700 m.
–3	50	8	4	
–4	50	8	3	
–5	50	8	2	ca. 750 m.
SETIA MULIA AREA				
<Ladang Padi>				
LP –1 –1	5*	2	1	Under foothill forest, steep
–2	10*	13	8	slope, ca. 500–700 m.
–2 –1	5*	5	3	
–2	5*	14	7	
–3	5*	4	4	
–3	5	8	–	
–4 –1	5	13	–	
–2	5	6	–	
–3	5	7	–	
–5 –1	5	5	2	
–2	5	14	9	
–3	5	18	10	
<Bt. Karang>				
BK –1	20*	18	14	Under foothill forest,
–2	10*	4	3	ca. 700–800 m.
–3	5*	3	3	On limestone, ca. 850 m.
AIRSIRAH AREA				
<Airsirah>				
AS –1	1000	25	20	Under hill forest, ground
–2 –1	5	3	–	flat, ca. 1000–1100 m.
–2	5	2	–	
–3	5*	1	–	
–4	5*	4	–	
BONDJOR AREA				
<Lurah Berangin Nat. Res.>				
LB –1	5	4	1	Lowland forest, ca. 450 m.
–2	20*	19	11	ca. 500 m.
Total		2374	919	

Sampling procedures represent either clones (*) or individual (no mark).

The plot is located at 550 to 595 m altitude, the full area being 0.9054 ha divided into 100 subplots (Fig. 23B). The growth of 456 individuals of *Schismatoglottis lancifolia* are recorded on the map. It seems that some crowded regions exist here and there from the mid-slope to the top of ridges, while some empty areas are found along small dales. Ecological or physiological features of this species may restrict their distributions.

Pinang Pinang plot—This is situated on a ridge extending to the southwest from the top of Mt. Gadut. This plot was established in August 1981, and is located on a gentle hill called Bukit Pinang Pinang, 490–520 m in altitude. The area is 1.0041 ha, which is subdivided into 115 subplots (Fig. 23A). The aspect of vegetation is almost the

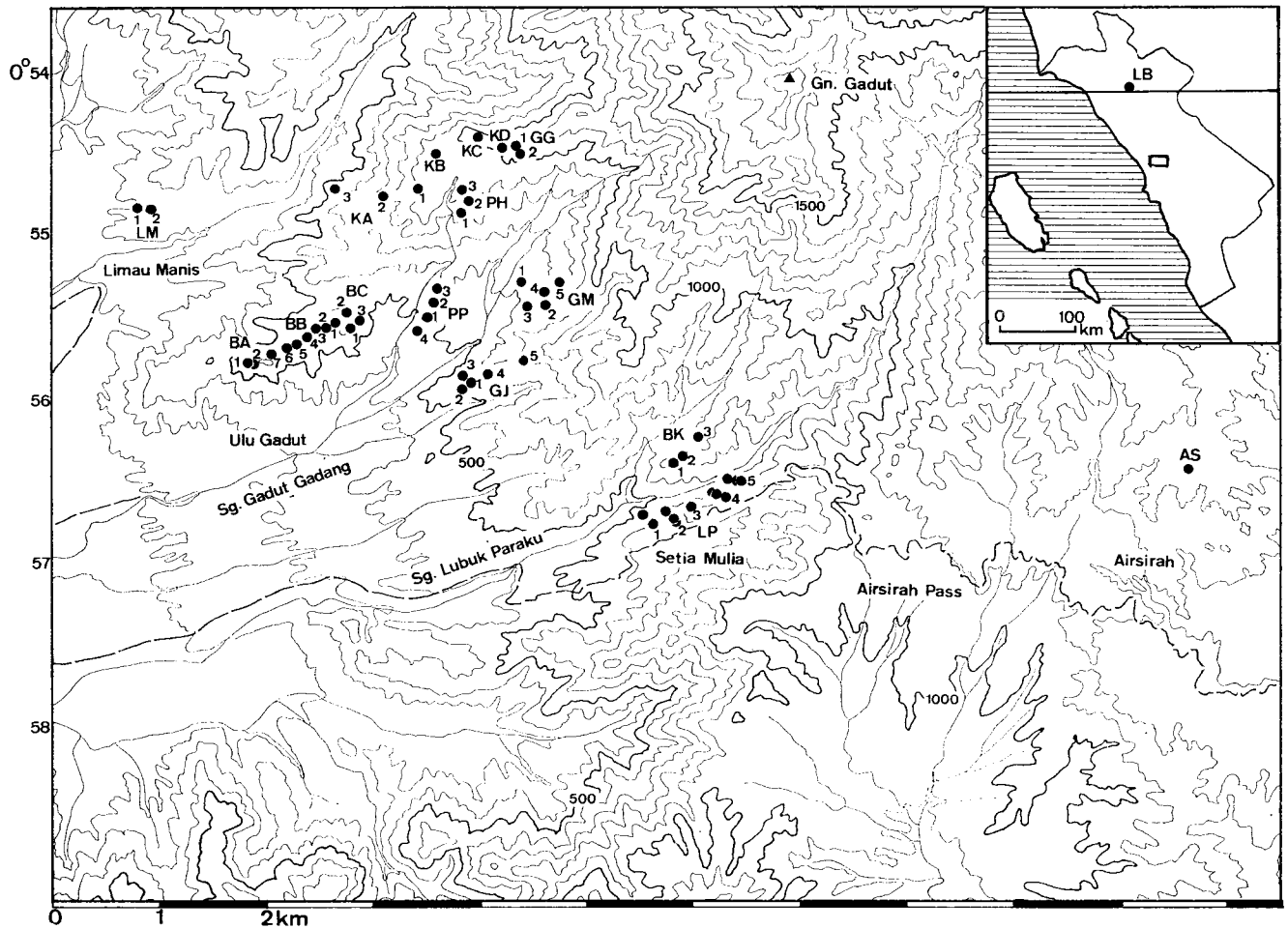


Fig. 1. The map of study sites at Limau Manis, Ulu Gadut, Setia Mulia, Airsirah and Bondjor area of West Sumatra. Capital letters and numbers are sampling locations and site which correspond to Table 1.

same as that of Gajabuih plot. In this plot 805 individuals of *S. lancifolia* are recorded in 1982. The distribution aspect is almost similar to Gajabuih plot. They grow densely on mid-slopes, but not at dales.

Pinang Pinang Atas Transect—This transect plot was established in August 1984 at the upper ridge of Pinang Pinang plot, and is stretched 370 meters length with 10 m width from top of the ridge to both sides of the stream. In the transect, 98 individuals are distributed from top to mid-slope, but no individuals grow in wetter mid- to lower slope. Three other species of *Schismatoglottis*, i.e. *S. batoensis*, *S. calyptrata* and *S. rupestris*, occur in lower slope of this transect.

Airsirah plot—This plot was established near Airsirah pass in September 1980, at an altitude of 1130 m, and the area was totaled to 961.09 m^2 with 10 subplots. The original vegetation type is the Hill Oak forest. As the plot is located at the highest marginal limit of this species, the individuals are rather rare compared with Gajabuih and Pinang Pinang plots, that is, only 25 individuals per ca. 1000 m^2. They are divided into 20 clones. Almost all of them are single clones.

The spatial positions of all individuals are recorded in these plots (Hotta ed., 1984, Appends. 7, 8, 9; Figs. 16, 21, 22). Other sites are situated on ridges of Mt. Gadut on elevations ranging from ca. 300 to 1100 meter. These are Bali Bukit, Bt. Batu Bajolang, Bt. Lantik, Bt. Kambut and Gn. Gadut, areas surround Bt. Gajabuih and Bt. Pinang Pinang, Setia Mulia and so on. Gn. Gadut site is located at the top of a ridge along the route from Pinang Pinang plot to the top of Mt. Gadut, which is approximately the highest habitat like as Airsirah plot. Usually all individuals of each site were collected, but in some cases one individual was collected as a representative of associating plants with exactly the same leaf characters. These associating plants were judged to be vegetatively reproductive clones which grew up from the axillary buds of fallen stem.

II. Polymorphic Characters and Definition of Clones

In tropical rain forest several plants are observed to have variation even in one area. Among them, *Schismatoglottis lancifolia* expresses remarkable variations in phenotype and karyotype even in a small colony (Plate I-A), such as red color pigment and white mottle on leaf, spathe color, leaf shape, size, rate of petiole vs. blade of leaf, satellite chromosome, B-chromosome and so on. These variations are conspicuous as classical herbarium taxonomists have recognized them in this species. Here, we describe these characters in detail.

1. Phenotypic Characteristics.

In the present study, red pigment and white mottle on leaf were fully examined. We can easily obtain sharp results from both characters, while it is difficult to observe in the field the other characters which show polymorphism and are flexible in culture conditions.

Petiole and leaf beneath color—The petiole and epidermis of beneath of this species has an anthocyanin type red color (Plate I-A). This type of red color leaves are sometimes

observed in forest floor herb in tropical rain forest (Burtt, 1977). It seems that the degree of the red color ranges from pale to deep. We picked up only the presence or absence of red color for statistical analysis, because the details of this character may change by age or growth condition. Indeed very small individuals sometimes do not fully express their leaf color and mottle. Four categories are distinguishable by the combination of petiole color and beneath color of leaf blade; i.e., individuals with red petioles and red beneath (RR), those with red and green (RG), those with green and red (GR) or those with green and green (GG). The third type (GR) is very rare.

Leaf mottle—Besides leaf color, this species expresses also polymorphism in leaf mottle (Fig. 2). The existence of mottle varies from none to whole, covering the whole surface of leaves. We categorize the degree of mottle into four classes; G, W1, W2 and W3. G category corresponds to leaves without mottle, while W3 indicates the mottle on nearly whole surface (Plate I-B). Individuals with mottle on the whole surface were rarely found at Pinang Pinang plot and its surroundings, e.g. four individuals observed at subplot No. 32 growing side by side were considered to have propagated by vegetative reproduction. The presence of the mottle does not mean the absence of chloroplast in the tissue in this species. Actually chloroplast is found in palisade cells as well as the cells of the tissue without mottle. The difference between the presence or absence of mottle is only in the arrangement of cells between epidermis and palisade tissue. The cells in non-mottle leaves are regularly packed (Fig. 3A),

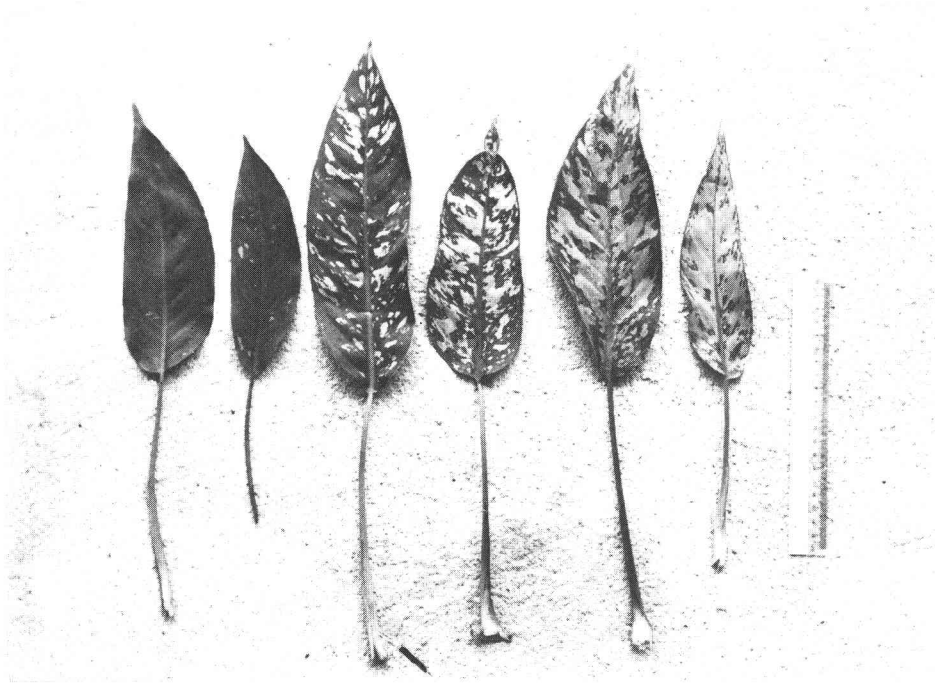


Fig. 2. Photograph showing polymorphism of leaf mottle of *Schismatoglottis lancifolia*. From left to right, G, G, W1, W2, W2 and W3.

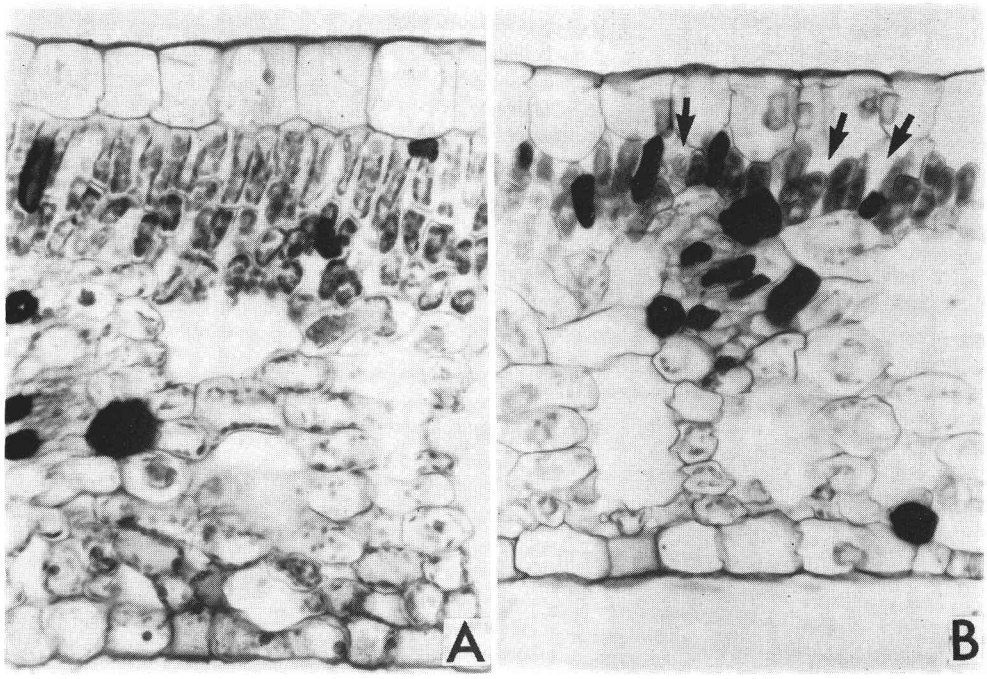


Fig. 3. Cross section of leaf (×80). A, unmottled leaf; B, mottled leaf; arrow, intercellular space.

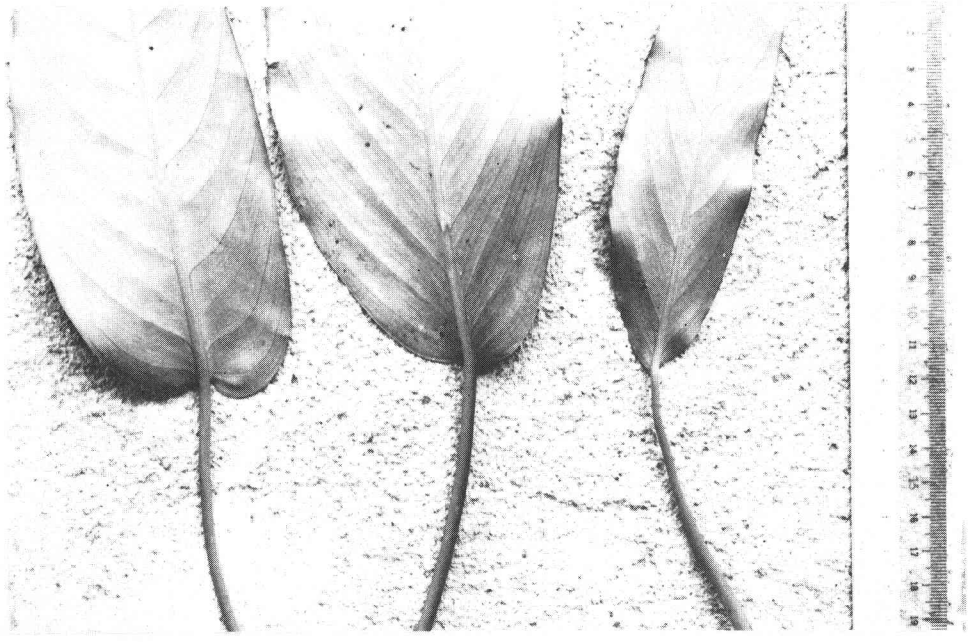


Fig. 4. Photograph showing polymorphism of leaf base. From left to right, cordate (CR), rotundate (RO) and cunnate (CN).

while those in mottle leaves are loose and have intercellular space between epidermis and palisade tissue (Fig. 3B). This type mottled leaf is often found in forest floor herbs in tropical region (Burtt, 1977) and temperate region, for examples, *Arisaema* spp., *Heterotropa* spp., *Polygonum* spp., *Anemone* spp., *Cirsium* spp., *Ainsliaea* spp., *Erythronium* spp., *Trillium* spp., and so on. The biological significance of mottle is still obscure, though it might suggest some adaptive meanings in both regions. In grassland population of *Trifolium repens* has this type mottle which occupies certain area by sheep grazing pressure (Cahn & Harper 1976a, b). In addition to the mottle, many stomata are observed on the surface of such leaf blades.

Leaf base—The shape of leaf base is also polymorphic in this species, varying from cordate to cunnate. The shape of the leaf base changes continuously, and it seems that they have some correlation with age or size. We categorized them into three types, cunnate (CN), rotundate (RO) and cordate (CR) (Fig. 4). For further detailed description of this characters, genetical analysis is required.

2. Karyological Characteristics.

The chromosome numbers of 919 of 2374 individuals were counted[1)] and almost all were found with 2n=26 and with 0–14 B-chromosomes (Table 3). This is the first report regarding this species. The basic chromosome number for this genus, *Schismatoglottis*, is to be x=13, judged from the evidences that 2n=26 in *S. batoensis*, *S. belophylla*, *S. okadai*, *S. rupestris* and *S. treubii* (Okada, unpubl.), *S. calyptrata* (Hotta, 1971), *S. concinna* Schott var. *immaculata* N. E. Br. (Marchant, 1970), *S. wallichii* Hook. f. (Marchant, 1970) and 2n=52 in *S. novoguineensis* (Linden) N. E. Br. var. *variegata* (Sharma & Bhattacharya, 1966) and *S. tecturata* (Schott) Engler (Marchant, 1970).

Triploid—The infraspecific polyploidy is found in two locations. Five individuals

Table 3. Number of individuals and their karyotypes

Location	Sites	JJ	JV	VV	Other	3x	B+	B−	Total
Limau Manis	LM	10	13	0			4	19	23
Bali Bukit	BA	10	5	0			6	9	15
Bt. Batu Bajolang	BB	24	17	2			14	29	43
Bt. Lantik	BC	15	19	0			17	17	34
Bt. Kambut	KM	15	11	2	1		14	15	29
Gn. Gadut	GG	10	5	0			2	13	15
Bt. Pinang Pinang	PP-1	69	59	6	4		41	97	138
	PP	49	52	8	1		37	73	110
Bt. Gajabuih	GJ-1	189	128	21		5	115	228	343
	GJ	29	23	2			18	36	54
Bt. Gambir	GM	13	3	1			0	17	17
Ladang Padi	LP	21	19	4			14	30	44
Bt. Karang	LP	10	9	1			7	13	20
Airsirah	AS-1	7	9	0		4	2	18	20
Lurah Berangin	LB	13	0	0	1		1	13	14
Total		478	378	47	7	9	292	627	919

1) Chromosome techniques are refered to Okada (1984).

(two clones) at Gajabuih plot (p. 38, Fig. 16) and four individuals (one clone) at Airsirah plot have 2n=39 with 0–8 B-chromosomes (Fig. 6E), they are the triploid level of x=13. These triploid clones show their own karyotypic and phenotypic characteristics and are presumed to have originated from three places independently, and spread vegetatively over 1×1 meter. It is the very rare case that the original places occurred polyploidizations in natural population are recorded on maps. There is no clear parallelism between the remarkable phenotypic diversity and ploidy level. The phenomenon of the infraspecific polyploidization is observed in some other members of Araceae, such as, *Colocasia esculenta* with 2n=28 (2x) and 42 (3x), and *Xanthosoma lindenii* with 2n=26 (2x), 39 (3x) and 52 (4x) (Okada, unpubl.).

Satellite chromosome—A remarkable polymorphism of the large satellite chromosomes was found (Figs. 5, 6, 7A). One of the type possesses a 0.2–0.3 μm long satellite at the distal end of the short arm, and the primary constriction is located at the subterminal region (Figs. 5A, B, 7A). More than 90% of the individuals have one or two chromosomes of this type in the complement. Similar type of satellite chromosome is observed in *Schismatoglottis okadai* and *S. calyptrata* (Okada, unpubl.). This type of satellite chromosome may be common and original to the allied species and it is classified as "J".

The second type is a metacentric chromosome (Figs. 5B, C, 7A). The position of the primary constriction of this type is at the median region, being different from that of "J" type. The size of the whole chromosome is shortener to some degree. It possesses the characteristic secondary constriction at the proximal region of the short arm close to the primary constriction. The frequency of this type in populations is less common than "J" type, about 40% individuals possess one or two chromosomes of this type. This type is named as "V".

The third type is the largest chromosome in this species (Fig. 6A). Very small

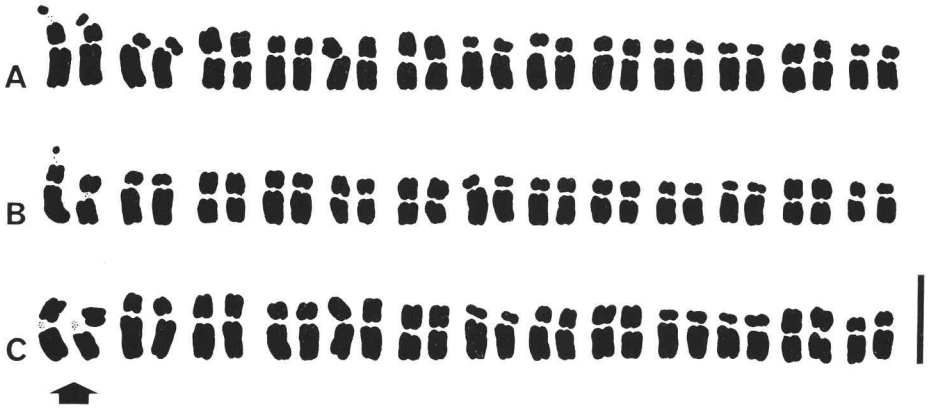


Fig. 5. Somatic metaphase chromosomes. 2n=26. A, the complement with two J type satellite chromosomes; B, the complement with J and V; C, the complement with two V. Arrow, satellite chromosome, bar=5 μm.

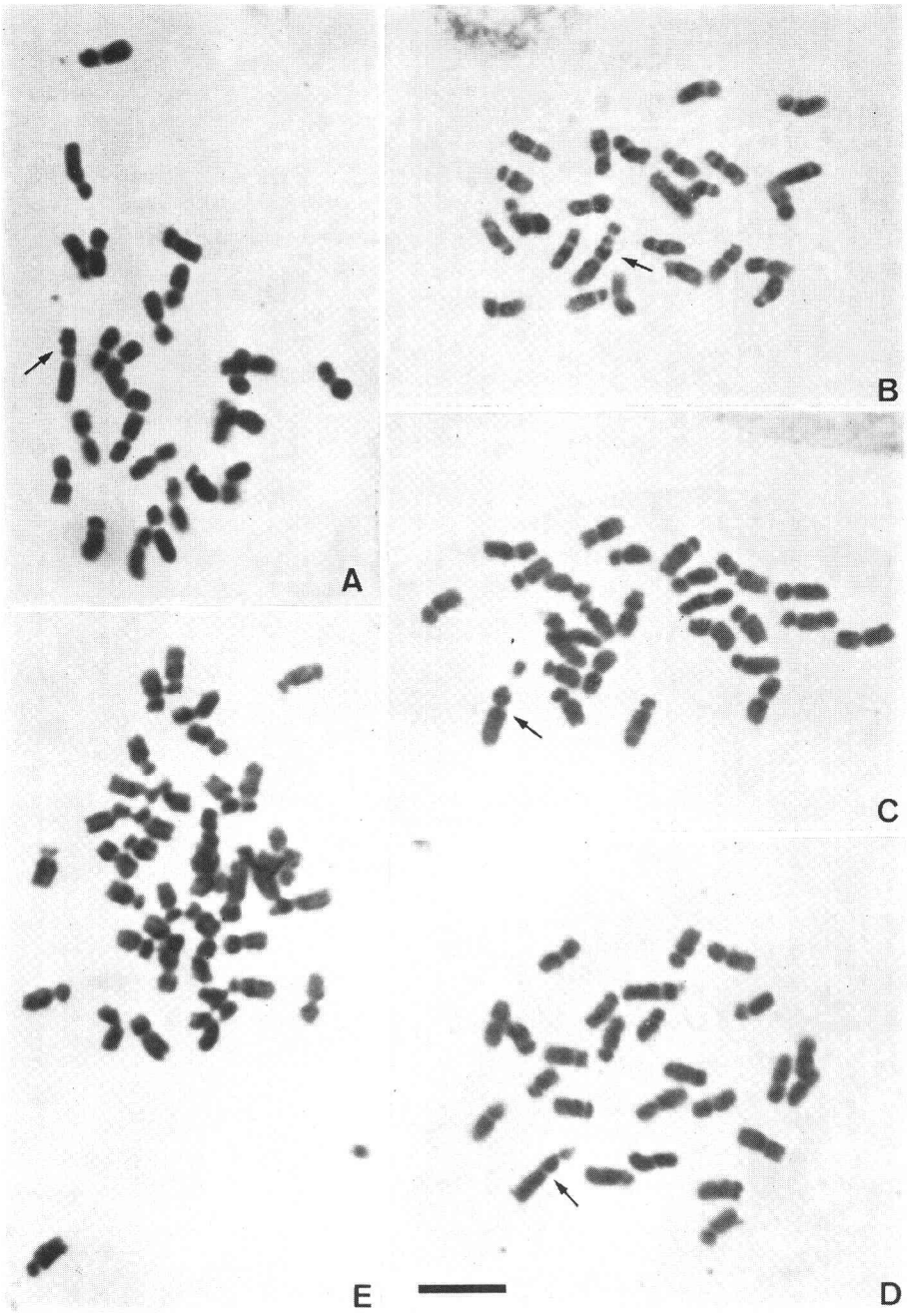


Fig. 6. Microphotographs showing variations of karyotype. A, third type of satellite chromosome; B, fourth type; C, fifth type; D, sixth type and E, triploid (2n=39). Arrow, satellite chromosome; bar=5 μm.

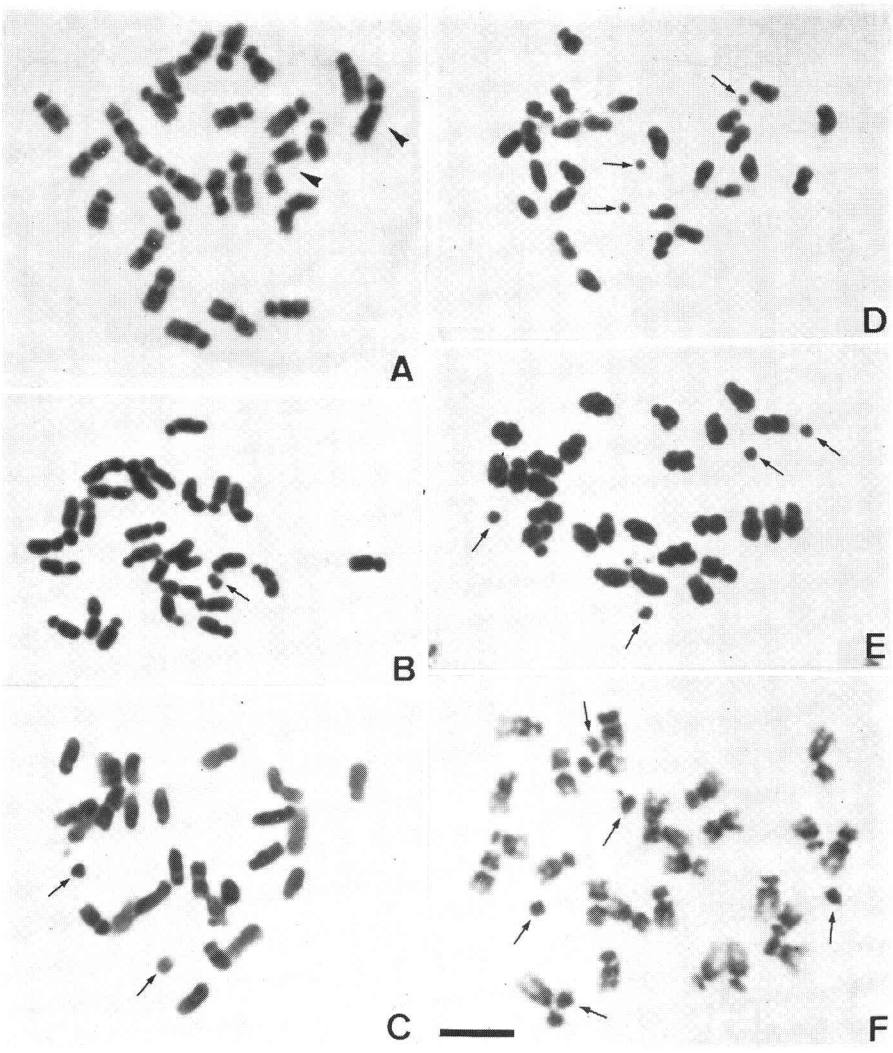


Fig. 7. Microphotographs of somatic chromosomes. 2n=26+0−5B. A, heterogeneous set with J and V type satellite chromosomes (arrow heads) without B-chromosome; B-F, cell with B-chromosomes (arrows). B, 1B; C, 2B; D, 3B; E, 4B; F, 5B. Bar=5 μm.

satellite is located at the distal end of the short arm, and the primary constriction is submetacentric. This type is found only in two individuals at subplot No. 70 of Pinang Pinang plot.

The fourth type is also a very large chromosome with two secondary constrictions at the interstitial parts of the short arm, and the primary constriction is located at the middle part of chromosome (Fig. 6B). This type is also very rare, and found only in two individuals at subplot No. 35 of Pinang Pinang plot. In these individuals another satellite chromosome is not observed.

The fifth type is found at Pinang Pinang Atas plot. The primary constriction is located at the subterminal region. It has a very large satellite, about 0.5 μm, at the distal end of the short arm (Fig. 6C). Except for its large satellite, this chromosome is morphologically similar to the first type.

The sixth type has a peculiar satellite at the distal end of the short arm, which is separated into two parts (Fig. 6D). The primary constriction is located at the subterminal position, like that in the first type. This type is found in one individual from Bondjor.

As the third, fourth, fifth and sixth types are minor elements of the mutations of satellite chromosome, they are not used for population analysis.

The frequent appearance of mutation in the morphology of satellite chromosomes and in ploidy level suggests that the favorable environment under tropical rain forests allows survival of many kinds of mutations, or these mutations do not affect viability very much. It is very interesting to analyze the chromosome behavior at meiosis or the pollen grain fertility on these mutants. Pollen fertility of a few individuals with homogeneous and heterogeneous sets of J and V type were examined. Usually, the organisms with heterogeneous chromosome sets, except sex chromosomes, become less fertile and extinct or minority in population. Nevertheless individuals of *S. lancifolia* with both homo- and heterogeneous sets of J and V type do not exhibit any significant difference in pollen grain fertility, 96% in homogeneous individuals and 95% in heterogeneous ones, respectively. More detailed observations are required.

B-chromosome—About one third of individuals observed possess very small size chromosomes of approximately 0.2–0.4 μm in length (Figs. 7B-F). They are variable in number ranging from 0 to 14 among cells within the same root tip as well as between individuals. The numerical variability of B-chromosome in the same individuals is reported by Bjorkman (1951) in *Agrostis canica* in which root no. 3 of clone no. 2338 shows variation ranging from 2 to 13. Grun (1959) also observed the same phenomenon in *Allium cernuum* Roth, where many individuals and tissues possess numerical variability of B-chromosome among cells ranging from 0 to 3, 1 to 4, 5 to 11 etc. These peculiar behaviors are one of the very important characteristics for the definition of B-chromosome as well as for the abnormal behavior at meiosis (Jones & Rees, 1982). On the basis of the fact that these small chromosomes are variable in number within the same individuals, they are defined as B-chromosomes. There is no correlation between the distribution of B-chromosome and phenotypic diversity. The occurrence of such chromosome behavior at meiosis have not yet been observed. These B-chromosomes are considered to exist persistently in the common ancestral stocks of all allied species on the basis of the evidences that *Schismatoglottis concinna* (Marchant, 1970), *S. rupestris* and *S. okadai* (Okada, unpubl.) also possess similar shaped B-chromosomes in some individuals. The same phenomenon of the numerical variations on B-chromosome is also observed in *S. okadai*. Individuals with large number of B-chromosome show great numerical variability, while those with no or 1 B-chromosome are stable (Fig. 8). Therefore, the criteria of the presence or absence of B-chromosome is used for the population analysis.

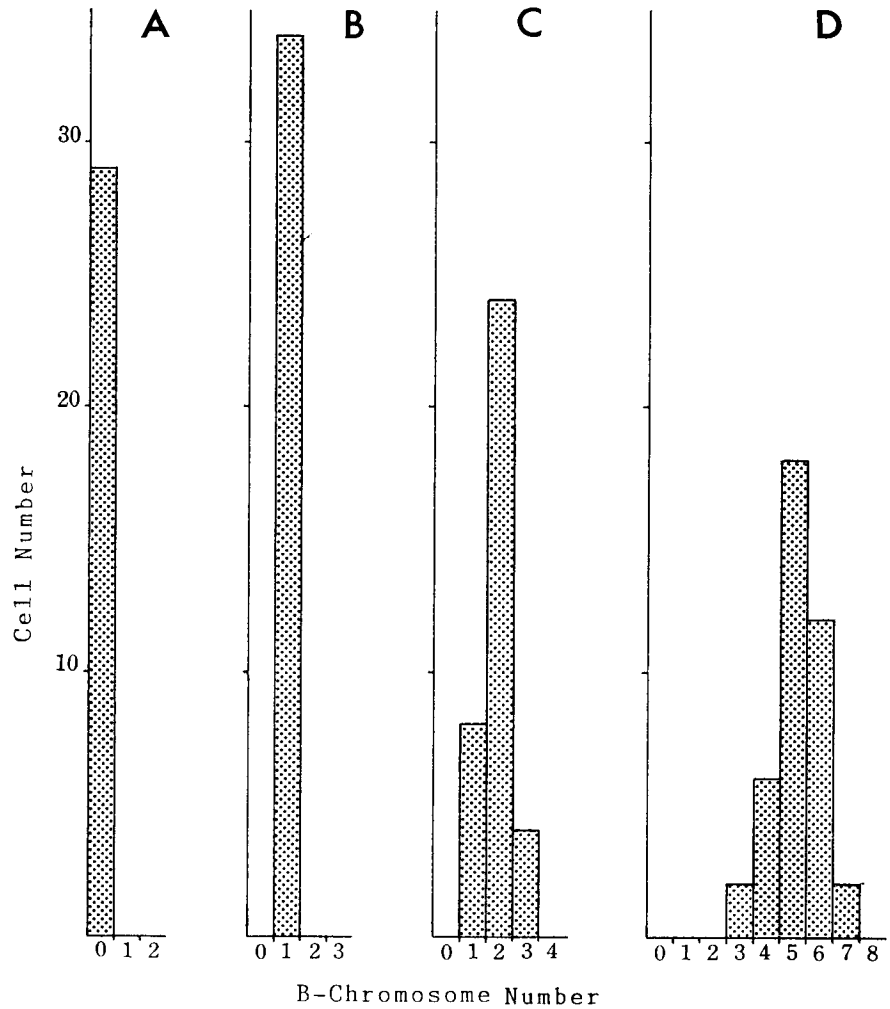


Fig. 8. Diagram showing the numerical variability of B-chromosomes in the same individuals. Individuals with no (A) or few (B) B-chromosome show stability in number, while those with high number (C, D) are variable in number.

3. Relationship between Phenotypic and Karyotypic Characteristics

Schismatoglottis lancifolia has many polymorphic characters as mentioned above. Several combinations of these characters were found in the study sites even though the population is rather small. To analyze the relation between leaf and karyological characters, chi square test was applied on the Gajabuih plot population (Table 4). No correlation or link between these characters were detectable. These characters are undoubtedly regulated by genetic rule and seem to be inherited independently. Moreover, the behavior of autosomes (satellite chromosomes in this case) is generally not considered to correlate to B-chromosomes in mitotic cell division. Therefore, the polymorphisms of these characters are treated as independent factors for the analysis.

Table 4. Relationships between leaf character and karyotype.

A. Chi square test on color-karyotype in Gajabuih plot.
Numbers in bracket are expected values.

Color/Karyotype	JJ	JV	VV	Total	B+	B−	Total
Green	111(112.1)	93(88.9)	13(16.0)	217	75(72.3)	142(144.7)	217
Red	29(27.9)	18(22.1)	7(4.0)	54	16(18.7)	40(37.3)	56
Total	140	111	20	271	91	182	273

Calculated chi square value is 3.86016. Calculated chi square value is 0.71889.
Corresponding probability is 0.145366. Corresponding probability is 0.396507.
The difference is not significant P>0.05. The difference is not significant P>0.05.

B. Chi square test on mottle-karyotype in Gajabuih plot.
Numbers in bracket are expected values.

Mottle/Karyotype	JJ	JV	VV	Total	B+	B−	Total
Green	83(82.1)	64(65.1)	12(11.7)	159	55(53.3)	105(106.7)	160
Mottle	57(57.9)	47(45.9)	8(8.3)	112	36(37.7)	77(75.3)	113
Total	140	111	20	271	91	182	273

Calculated chi square value is 0.08339. Calculated chi square value is 0.18874.
Corresponding probability is 0.951614. Corresponding probability is 0.66396.
The difference is not significant P>0.05. The difference is not significant P>0.05.

4. Definition of Clones

In plants with vegetative reproduction in part, the identification of individuality, that is, the detection whether or not individuals are derived from the same seed, is a very important step for a real understanding of the population structure. It is very difficult to identify the clone when the species preserve both sexual and asexual propagation system. Fortunately this species contains several genetic variabilities on many characters, and individuals show a lot of combinations of them, so we use the phenotypic and karyotypic aspects for the recognition of clones. Here after individuals that were found to be totally different from the surrounding plants on phenotypic and karyological aspects will be called "single clone". Those that show a homogeneous phenotype and karyotype and are located close to each other will be called "plural clone" (Plate I-B). At Gajabuih, Pinang Pinang, Pinang Pinang Atas and Airsirah plots single and plural clones were identified on the bases of combination of these characters and spatial arrangements.

In both Pinang Pinang and Gajabuih plots, the ratio of individuals per one clone is very low, about 1.6, with very heigh ratio of single clone (67 and 74% respectively) and rare exception of the maximum clone with 14 individuals (Fig. 9) which occupies about 30 m^2. This suggests that vegetative reproduction is not an efficient system of propagation in this species and most of them are reproduced sexually.

III. Reproductive Aspect of *Schismatoglottis lancifolia*

For the studies of population or evolutionary biology, analysis of reproductive aspect is one of the most important factors. The reproductive system has an enormous

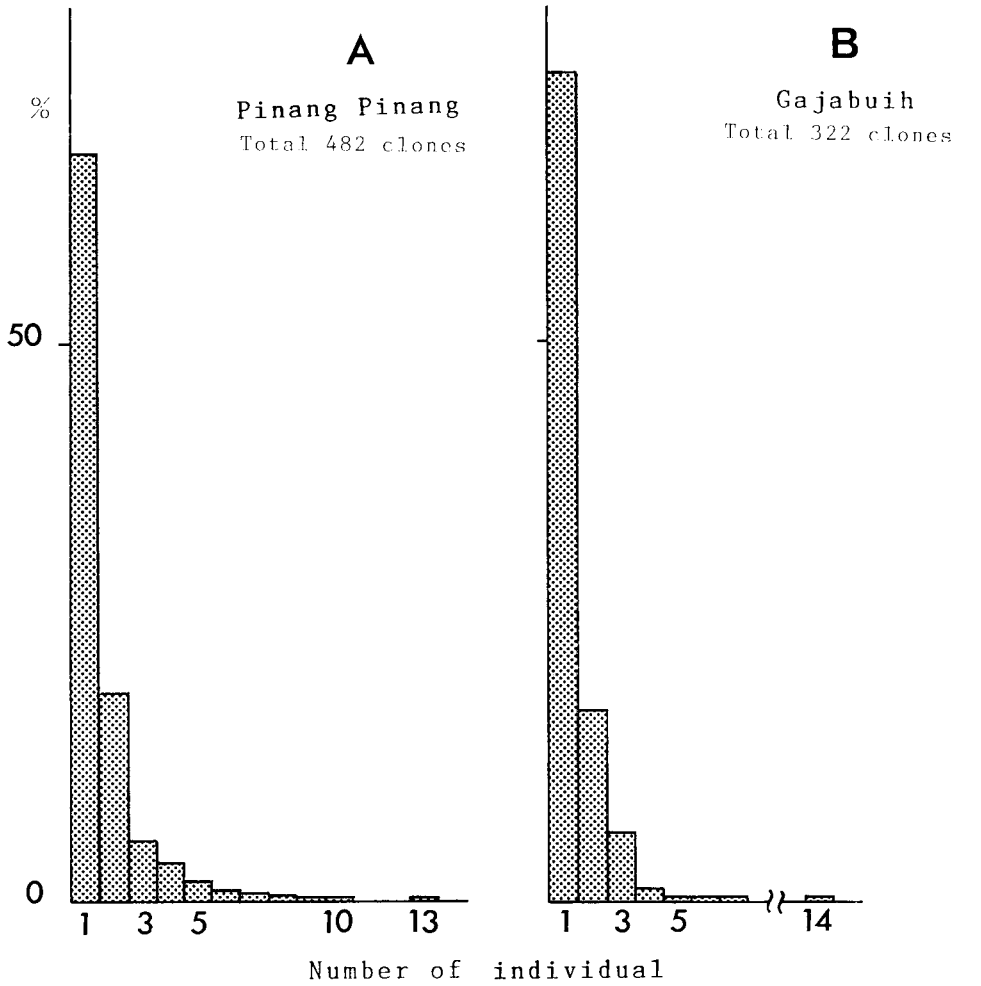


Fig. 9. Distribution frequency of each clone class expressing by individual number. Clone becomes larger frequency fewer. A, Pinang Pinang; B, Gajabuih.

influence on variation, structure, and fitness of the species or population (Willson, 1983). There are few organisms which have been studied in this aspect in tropics.

1. Flowering Schedule

From our 5 years (1980–1984) field observation, *Schismatoglottis lancifolia* is presumed to flower usually twice in a year; once from the end of January to the end of February in the midst of the driest period, and another in August though a dry season, but, fewer flowering individuals were observed in this period. The inflorescence, spadix, is enclosed in spathe like structures as in the case of almost all Araceae. The spadix consists of four parts; the basal female part, the middle male part, the sterile part between the formers and the apical sterile appendage (Fig. 10D). The spathe is differentiated into tube and lamina, the former (spathe tube) being green or reddish purple, like the lower

surface of leaf, and the latter (spathe lamina) being white or reddish. Both the spathe color and leaf color are perhaps regulated by the same gene system. The inner surface of the spathe is very smooth. Flowering sequence of female and male flowers is different, i.e., protogyny. Before flowering, the spathe is completely close (Fig. 10A). When female flowers mature in day time, the lower part of the spathe tube opens and the female flowers are visible from outside. In the evening of the same day, the spathe tube closes. At this stage the male flowers are still immature and spathe lamina

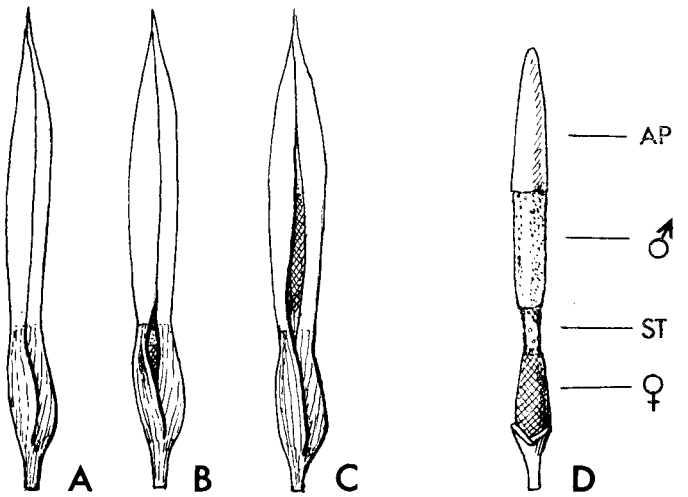


Fig. 10. Inflorescence showing the flowering schedule and structure. A, before anthesis; B, female phase (1st. day); C, male phase (2nd day); D, the structure of spadix. ♀, female part; ♂, male part; AP, appendage; ST, sterile part. Scale=1 cm.

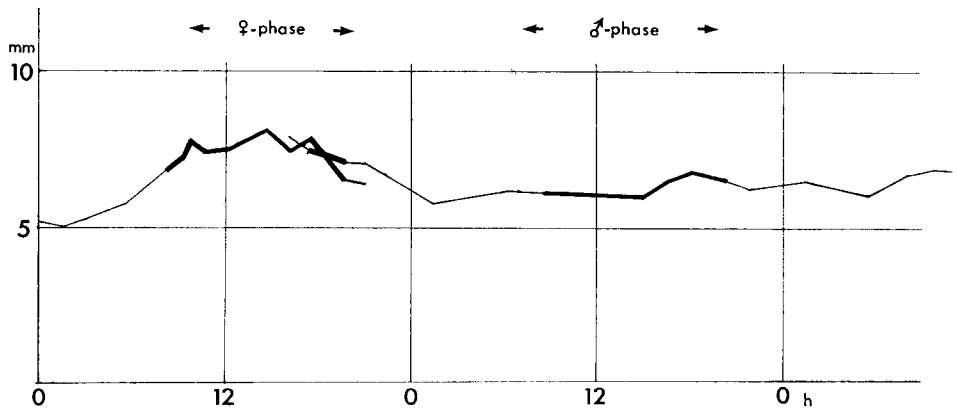


Fig. 11. Temporal change of spathe diameter at middle sterile part (ST in Fig. 10D) at anthesis during Feb. 14–16, 1983. Bold lines indicate opening of spathe in female or male part. At the first of ♀-phase, spathe at female part begins opening and spathe diameter at sterlie part increases. At evening the spathe closes. At next morning spathe at male part begins to open, however, sterile part tightly closes and the spathe diameter at sterile part does not tend to increase.

encloses them tightly (Fig. 10B). On the next day the spathe lamina opens, and the male flowers supply pollen grains. In this period, the fertility of the stigma of pistils are already reduced and spathe tube is closed at the middle sterile part of spadix. Therefore, pollens cannot go down to the female part (Fig. 10C). Figure 11 shows the changing of spathe diameter at the sterile part between the female and male parts. The spathe is closed at the sterile part except in the female phase. Because of these flowering behavior, inbreeding in the same inflorescence is completely impossible. The same flowering behavior, i.e., male flowers mature one day after the female phase, is known in *Philodendron* (Gottsberger & Amaral, 1984).

Though there is still low possibility of cross-fertilization between the inflorescences belonging to the same individual or clone, self incompatibility is observed in preliminary cross examination. Due to the above reason it is suggested that *Schismatoglottis lancifolia* keeps a typical outcross pollination.

From the field observations, the pollinators of this species are some small forest flies (Diptera) or small beetles which are supposed to move in a narrow range.

2. Seed Size, Dispersal and Germination

After flowering, the peduncle is bending and the spathe lamina and male part fall down together. Seed size of this species is small, 0.5 mm long and 0.2 mm wide. In a fruit 1–5 ellipsoidal seeds are enclosed with pericarp together. This small fruit is a unit of dispersal. When fruits mature, the spathe tube is broken and the fruits fall down. Juicy pericarp is probably attractive to dispersers. In *Schismatoglottis rupestris* and *Colocasia* sp. (Araceae), it is known that this type of small fruits are dispersed by ants (Hotta, unpubl.; Hambali, personal communication). The seeds are dispersed only a short distance around parental plants by this system.

The mature green seeds have chloroplast and show no dormancy. It is suggested that they can germinate with enough light. These seeds germinated a few weeks after they were sown in pots at Padang city, located near the study site. Seeds from heterogeneous parents also germinate very well. Preliminary experiments suggest that the germination rate is high, however, the death rate in juvenile stage is very high because of their small size. About 80–90% of safely germinated seedlings die suddenly by fungus attack or by blue green algae (Cyanophyta). Moreover the forest floor covered by fallen leaves and a few weeks of dry period is very unfavorable for the survival of seedlings.

IV. Variation in Plot

We have established six plots in Mt. Gadut area for the study of forest ecology. *Schismatoglottis lancifolia* occurs in five of these plots and has been studied in details in four plots, Pinang Pinang, Pinang Pinang Atas, Gajabuih and Airsirah plots. The record of their spatial positions and the identification of clone in four plots provide sufficient clue for the following. In addition, the tree species and some environmental conditions in plots are analyzed.

1. Size Distribution

Size distribution represented by stem diameter is shown in Figure 12. Low frequency of small, less than 2 mm, might be caused by the incomplete samplings of seedlings. Size distribution shows a peak at 6–8 mm diameter. Two factors perhaps contribute to the size distribution. One may rise from the effect of reverse progress of size. In case of forest floor perennials, descending of plant sizes often occurs due to nutrient conditions (Kawano, 1975). The other reason is vegetative reproduction. When plants reproduce vegetatively the size of their offsprings sometimes decreases. Judging from the similarity of this phenomenon between Gajabuih and Pinang Pinang plot in the case of both single and plural clones it can be said that this type size distribution may be common phenomenon in this species.

Individuals are presumed to start flowering at more than 7 mm of stem diameter, though sometimes flowering is observed when stem diameter is 5 mm. There are some

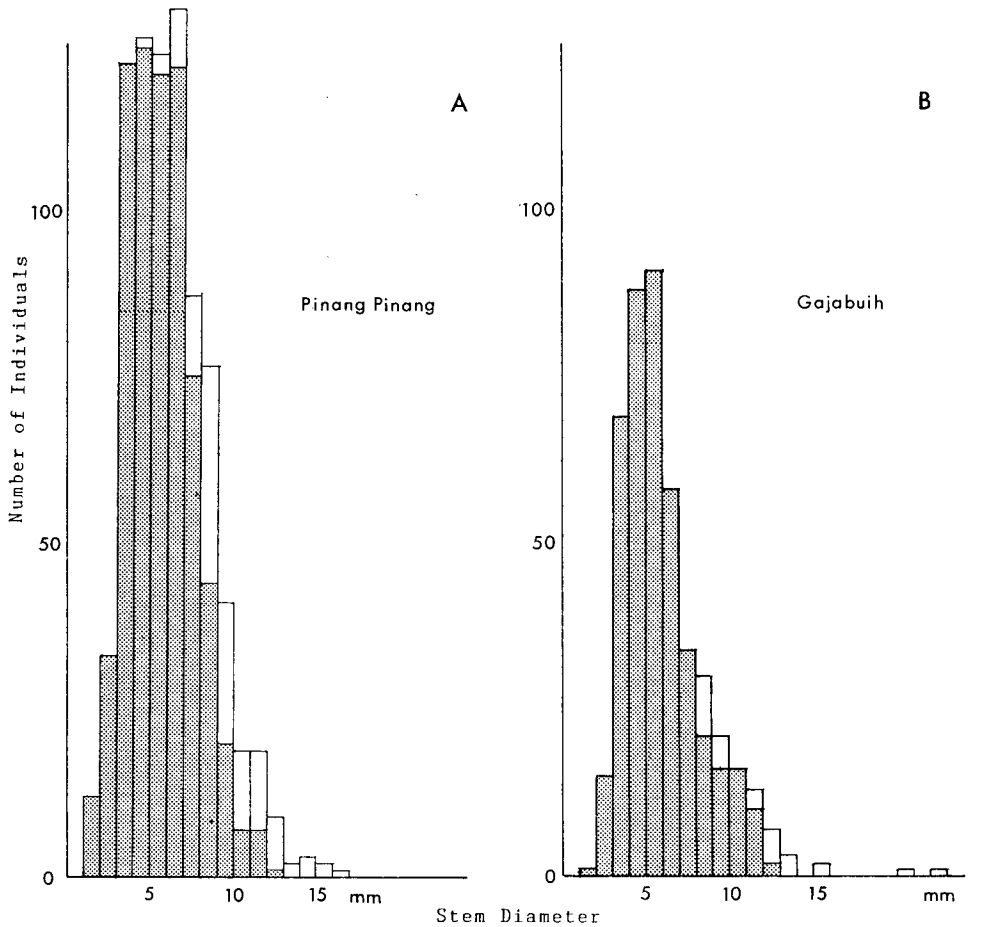


Fig. 12. Distribution number of stem diameter of individuals in Pinang Pinang (A) and Gajabuih (B). Dotted, no flowering individuals; open, flowering individuals.

differences in the distribution pattern of flowering individuals between the two plots (Fig. 12). The individuals of Pinang Pinang plot start flowering from rather smaller size and are observed more frequently than those of Gajabuih plot. It is assumed that this might be due to environmental difference between the two plots.

For the sake of statistical analysis of the correlations between leaf character and plant size, they are divided into 6 classes. The first four classes belonging to single clone, divided on the basis of stem diameter, are those i) 2–4 mm, ii) 5–7 mm, iii) 8–10 mm and iv) 11 mm and above, and the last two classes belonging to plural clone are; the clones consist of 2 individuals and those with more than 2 individuals. As small individuals categorized into class "i" are considered to not fully express their phenotypes, therefore the statistical data of this class is carefully analyzed.

2. Morphological Characteristics

Petiole and leaf beneath color—Four types of individuals are distinguishable on the basis of the combination of color of petiole and beneath of leaf blade as mentioned above, i.e., RR, RG, GR and GG. Figure 13 shows the correlation between the classes categorized on the basis of size and the frequency of the four types at Gajabuih and Pinang Pinang plots. In both plots, except for GR, the ratio of the first 3 categories is very similar. The combination of GR is not a comparable factor for its rare appearance in populations. Statistically, there is no significant differences between the classes. This

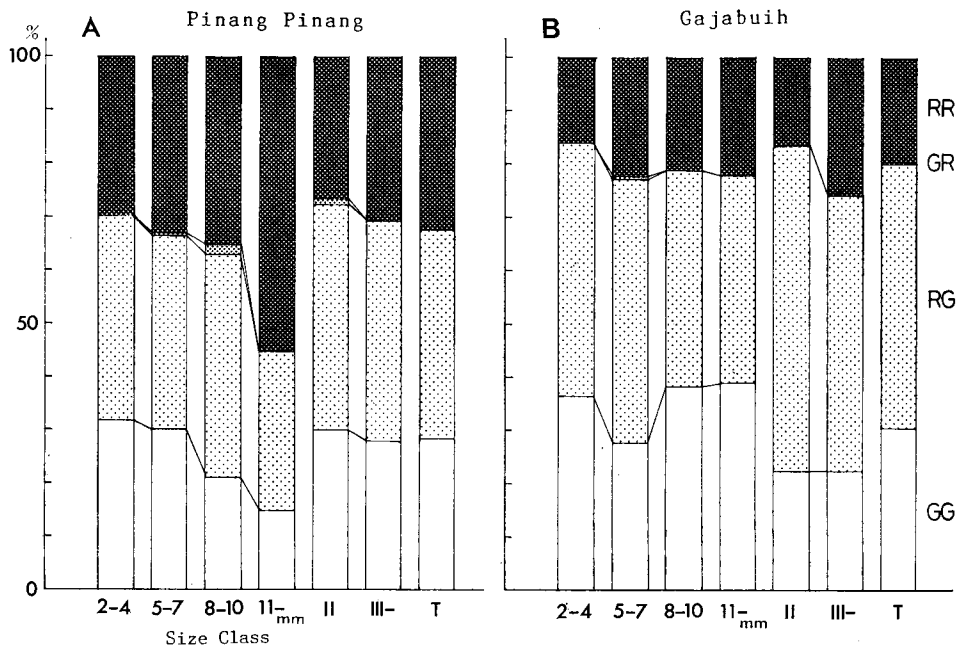


Fig. 13. Ratio of leaf color phenotype in each size class at Pinang Pinang (A) and Gajabuih (B). Densely dotted, RR; moderately dotted, GR; thinly dotted, RG; and open, GG. Class size, refer to text.

indicates that all phenotypes are viable evenly irrespective of their size. While, there seems to be a tendency that green petiole (GG+GR) decreases by age in both single and plural clones, it increases vegetative reproduction phase. There is no significant differences between plots. Also, there are no differences between the calculation based on a individual and clone.

Leaf mottle—There are many varieties of leaf mottle. The amount and pattern of leaf mottle is rather constant within a plant and is regulated genetically. For example, W3 type individual at subplot No. 32 of Pinang Pinang plot grew side by side and were considered to have propagated by vegetative reproduction. Triploid clones also display their own characteristic leaf mottle. This character varies rather qualitatively than quantitatively, we divide this variable characters into two categories, i.e., presence or absence of mottle, for simplification. Similar to the leaf color variation, the ratio of mottle leaf is not significantly different between individuals and clones. Further, the difference of ratio of mottle clone among size classes is not significant (Fig. 14). The ratio of mottle clone in four plots is almost the same.

To analyze the relation between leaf beneath color and leaf mottle, chi square test was carried out on Pinang Pinang and Gajabuih population taking basic unit as a clone. No significant correlations between the populations of the two plots was detected (Table 5). Both characters are inherited independently.

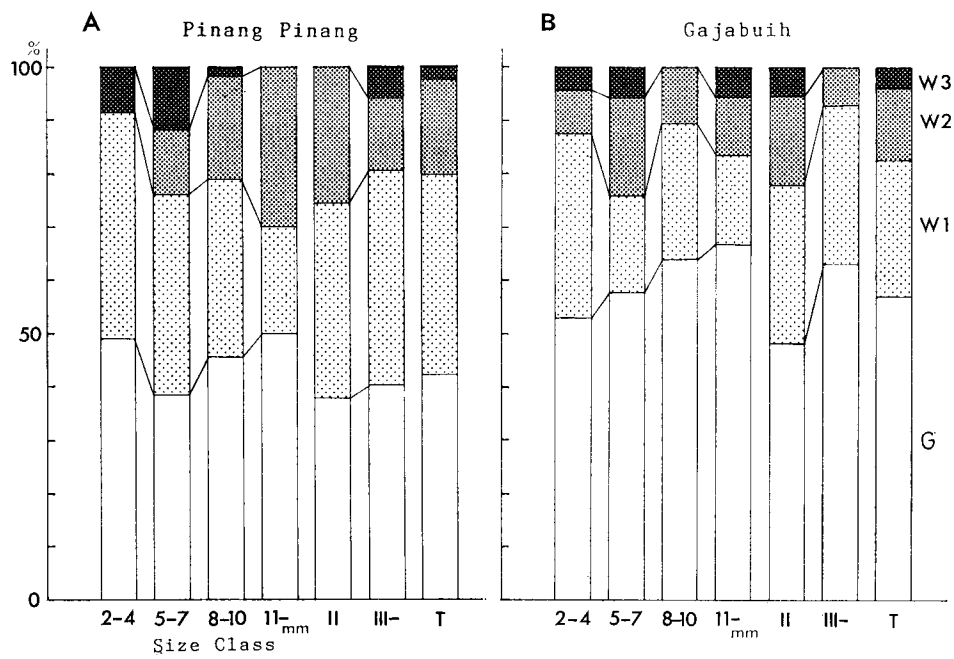


Fig. 14. Ratio of leaf mottle phenotype in each size class at Pinang Pinang (A) and Gajabuih (B). Densely dotted, W3; moderately dotted, W2; thinly dotted, W1; and open, G. Class size, refer to text.

Table 5. Relationship between two leaf characters

A. Chi square test on mottle-color in Pinang Pinang plot.
Numbers in bracket are expected values

Mottle/Color	Green	Red	Total
Green	139 (137.6)	65 (66.4)	204
Mottle	186 (187.4)	92 (90.6)	278
Total	325	157	482

Calculated chi square value is 0.08115.
Corresponding probability is 0.7757.
The difference is not significant $P>0.05$.

B. Chi square test on mottle-color in Gajabuih plot.
Numbers in bracket are expected values

Mottle/Color	Green	Red	Total
Green	150 (145.5)	33 (37.5)	183
Mottle	106 (110.5)	33 (28.5)	139
Total	256	66	322

Calculated chi square value is 1.57957.
Corresponding probability is 0.20882.
The difference is not significant $P>0.05$.

3. Morphological Characters and Microhabitat

The richness of species diversity in tropics is interpreted to result from the richness of ecological niche which shows a patch distribution pattern. In this case, there is a possibility that the phenotypic polymorphism might be due to this effect. Therefore, the frequency of each phenotype in graded environmental condition is analyzed in order to know whether there is a correlation between microhabitat and leaf phenotype or not. There are many factors such as light, water, nutrient, CO_2 density etc. which severely limit the survival of plants (Harper, 1977). Among them, it is considered that the most important factors for the survival of forest floor herbs in tropics are light intensity and moisture. Fortunately, the following environmental parameters are available in Pinang Pinang and Gajabuih plots;

1) Soil moisture (Figs. 15A, B) was measured by Wakatsuki et al. (1984) by gypsum block moisture sensors during December to February 1983. This season is one of the driest period in this area (Table 1). Soil moisture in the two plots is categorized into three ranks, wet, moderate, and dry. The 'dry' condition is indeed very wet compared with other tropics. A few dry subplots exist in Pinang Pinang plot but, since their number is small, they are considered to be insufficient number for statistic analysis.

2) Abundance of secondary tree species (Figs. 15C, D). By the distribution data of tree species of secondary forest element (Ogino et al., 1984), the subplots are divided into 1) species absent, 2) one species present, 3) more than two species. The tree species are as follows; *Antocephallus indicus* Rich., *Evodia latifolia* DC., *Grewia paniculata Roxb.* ex DC. (=*Microcos florida*), *Macaranga denticulata* (Bl.) M. A., *M. gigantea* M. A., *M. hypoleuca* M. A., *M. pruinosa* M. A., *M. triloba* (Reinw. ex Bl.) M. A., *Mallotus pani-*

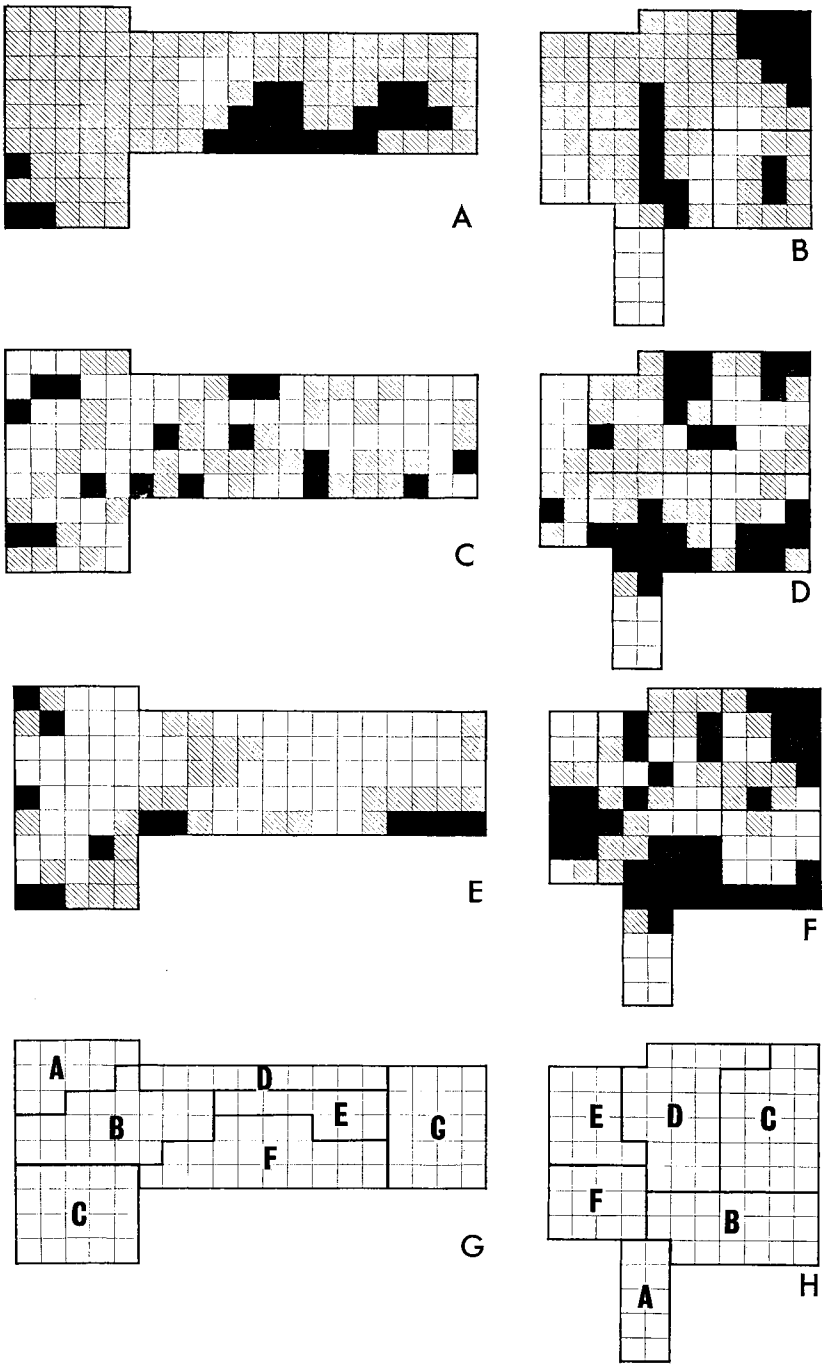


Fig. 15. Environmental conditions in Pinang Pinang (A, C, E, G) and Gajabuih (B, D, F, H) plot. A & B=Soil moisture, filled, wet; hatched, moderate; open, dry. C & D=Abundance of secondary tree species, filled, more than 2 spp.; hatched, 1 spp.; open, absent. E & F=Coverage of subplot, filled, open; hatched, moderate; open, close. G & H=Topographical grouping.

culatus (Lmk.) M. A., *Eurya acuminata* DC., *Shima wallichii* (DC.) Korth., *Styrax paralleloneurum* Perk, *S. serrulatum* Roxb., *Trema angustifolia* (L.) Bl., *Vitex gamosepala* Griff., *Villebrunea rubescens* (Bl.) Bl. This ranking seems to correspond to the stage of succession of the gaps, which may reflect the period from some event of disturbance.

3) Coverage of subplot (Figs. 15E, F). This parameter indicates light intensity at the time of study. Subplots are categorized into three ranks, continuous canopy present, edge of gap, and gap (Hotta et al., 1984b).

In addition to these parameters, spatial and topographical grouping is also applied for analysis (Figs. 15G, H).

The result of chi square test on correlation between these parameters and frequencies of characters is shown in Table 6. The result shows no significant differences between two parameters, except in two cases, soil moisture—leaf mottle in Pinang Pinang plot and coverage—leaf mottle in Gajabuih plot. Regarding the soil moisture at Pinang Pinang plot, it was found that individuals with mottle leaf are more abundant in dry place than expected. However, as dry subplots are very few, this result is considered to arise from insufficient number of samples. While, individuals with leaf mottle are also more abundant in some degree at rough coverage in Gajabuih plot. The increase or decrease of the frequency of leaf mottle correlated with environmental gradient, however, does not appear constantly. The conflicting results between the two plots indicate that it might have occurred from some statistical error. It is concluded that there is no clinal changes of the ratio of leaf phenotype relation to the microhabitat examined here.

4. Cytological Analysis

A. Gajabuih plot.

In this plot the karyotype of 343 of 456 individuals were checked. They are classified into 280 clones, based on leaf character, karyotype and distribution (Table 7). Triploid clones at subplot No. 3 and No. 15 are one of the direct evidences for vegetative propagation. The clone at subplot No. 3 includes 2 individuals, while that of subplot No. 15 includes 3. The former possesses JVV complement and the latter JJJ (Fig. 16). The diploid clones distributed near each triploid clone have two corresponding satellite chromosomes, that is, No. 3–1 clone possesses JV vs. No. 3–2 clone JVV, and No. 15–2 clone JJ vs. No. 15–1 clone JJJ. They show the same leaf characters as well. It is natural to consider that these triploid clones occurred independently at each place.

Most of clones consist of one individual and categorized under single-clone (Fig. 9). The biggest plural clone at subplot No. 95 exceptionally consists of 14 individuals which spread over 5×10 m^2 area. In contrast to *Schismatoglottis okadai* (Okada, unpubl.) vegetative reproduction is not the main propagation system in this species. *S. okadai* forms densely crowded patches on rocks, while this species grows rather less densely. There are no significant statistical differences regarding karyological characteristics between single and plural clones, nor between the size classes (Table 8). It may suggest that the variations in both satellite chromosome and B-chromosome

Table 6. Chi square test on the correlation between leaf phenotypes and micro-environment
Numbers in bracket are expected values

A. Soil moisture.

Gajabuih plot.

	Leaf mottle		Leaf color		
	Green	Mottle	Green	Red	Total
Wet	49 (48.3)	36 (36.7)	71 (67.6)	14 (17.4)	85
Mod.	113 (113.7)	87 (86.3)	155 (159.4)	45 (41.0)	200
Dry	21 (21.0)	16 (16.0)	30 (29.4)	7 (7.6)	37
Total	183	139	256	66	322

Calculated chi square value is 3.2088. Calculated chi square value is 1.3946.
Corresponding probability is 0.9841. Corresponding probability is 0.4973.
The difference is not significant $P>0.05$. The difference is not significant $P>0.05$.

Pinang Pinang plot.

	G	M	G	R	Total
Wet	19 (17.4)	22 (23.6)	33 (27.6)	8 (13.4)	41
Mod.	161 (171.8)	245 (234.2)	272 (273.8)	134 (132.2)	406
Dry	24 (21.0)	11 (20.2)	20 (23.6)	15 (11.4)	35
Total	204	278	325	157	482

Calculated chi square value is 11.3335. Calculated chi square value is 4.9044.
Corresponding probability is 0.0035. Corresponding probability is 0.0861.
The difference is significant $P<0.01$. The difference is not significant $P>0.05$.

B. Abundance of tree species of secondary forest element.

Gajabuih plot.

	G	M	G	R	Total
Absent	47 (54.6)	49 (41.4)	78 (76.3)	18 (19.7)	96
1 sp.	69 (61.9)	40 (47.1)	87 (86.7)	22 (22.3)	109
2 sp.<	67 (66.5)	50 (50.5)	91 (93.0)	26 (24.0)	117
Total	183	139	256	66	322

Calculated chi square value is 4.2951. Calculated chi square value is 0.4001.
Corresponding probability is 0.1168. Corresponding probability is 0.8187.
The difference is not significant $P>0.05$. The difference is not significant $P>0.05$.

Pinang Pinang plot.

	G	M	G	R	Total
Absent	121 (114.7)	150 (156.3)	187 (182.7)	84 (88.3)	271
1 sp.	53 (60.1)	89 (81.9)	92 (95.7)	50 (46.3)	142
2 sp<	30 (29.2)	39 (39.8)	46 (46.5)	23 (22.5)	69
Total	204	278	325	157	482

Calculated chi square value is 2.9023. Calculated chi square value is 0.7749.
Corresponding probability is 0.3513. Corresponding probability is 0.6788.
The difference is not significant $P>0.05$. The difference is not significant $P>0.05$.

(cont'd.)

(Table 6. cont'd.)

C. Coverage of tree canopy.

Gajabuih plot.

	G	M	G	R	Total
Covered	40 (47.7)	44 (36.3)	73 (66.8)	11 (17.2)	84
Mod.	42 (51.5)	48 (38.9)	66 (71.6)	24 (18.4)	90
Gap	101 (84.1)	47 (63.9)	117 (117.7)	31 (30.3)	148
Total	183	139	256	66	322

Calculated chi square value is 14.5523.
Corresponding probability is 0.0007.
The difference is significant $P<0.01$.

Calculated chi square value is 4.9447.
Corresponding probability is 0.0844.
The difference is not significant $P>0.05$.

Pinang Pinang plot.

	G	M	G	R	Total
Covered	121 (119.8)	162 (163.2)	184 (190.8)	99 (92.2)	283
Mod.	64 (62.6)	84 (85.4)	110 (99.8)	38 (48.2)	148
Gap	19 (21.6)	32 (29.4)	31 (34.4)	20 (16.6)	51
Total	204	278	325	157	482

Calculated chi square value is 0.6097.
Corresponding probability is 0.7372.
The difference is not significant $P>0.05$.

Calculated chi square value is 4.9784.
Corresponding probability is 0.0830.
The difference is not significant $P>0.05$.

D. Grouping by patch and topography.

Gajabuih plot.

Sub.	G	M	G	R	Total
A	16 (20.5)	20 (15.5)	29 (28.6)	7 (7.4)	36
B	30 (25.0)	14 (19.0)	38 (35.0)	6 (9.0)	44
C	23 (26.7)	24 (20.3)	40 (37.4)	7 (9.6)	47
D	59 (63.7)	53 (48.3)	82 (89.0)	30 (23.0)	122
E	31 (26.7)	16 (20.3)	42 (37.4)	5 (9.6)	47
F	24 (20.5)	12 (15.5)	25 (28.6)	11 (7.4)	36
Total	183	139	256	66	322

Calculated chi square value is 9.5586
Corresponding probability is 0.0888.
The difference is not significant $P>0.05$.

Calculated chi square value is 9.9575
Corresponding probability is 0.0764.
The difference is not significant $P>0.05$.

Pinang Pinang plot.

	G	M	G	R	Total
A	36 (33.0)	42 (45.0)	59 (52.6)	19 (25.4)	78
B	15 (22.9)	39 (31.1)	38 (36.4)	16 (17.6)	54
C	42 (41.1)	55 (55.9)	67 (65.4)	30 (31.6)	97
D	19 (20.7)	30 (28.3)	30 (33.0)	19 (16.0)	49
E	24 (24.1)	33 (32.9)	39 (38.4)	18 (18.6)	57
F	36 (32.2)	40 (43.8)	48 (51.2)	28 (24.8)	76
G	32 (30.0)	39 (41.0)	44 (47.9)	27 (23.1)	71
Total	204	278	325	157	482

Calculated chi square value is 6.4527.
Corresponding probability is 0.3744.
The difference is not significant $P>0.05$.

Calculated chi square value is 5.2054.
Corresponding probability is 0.5178.
The difference is not significant $P>0.05$.

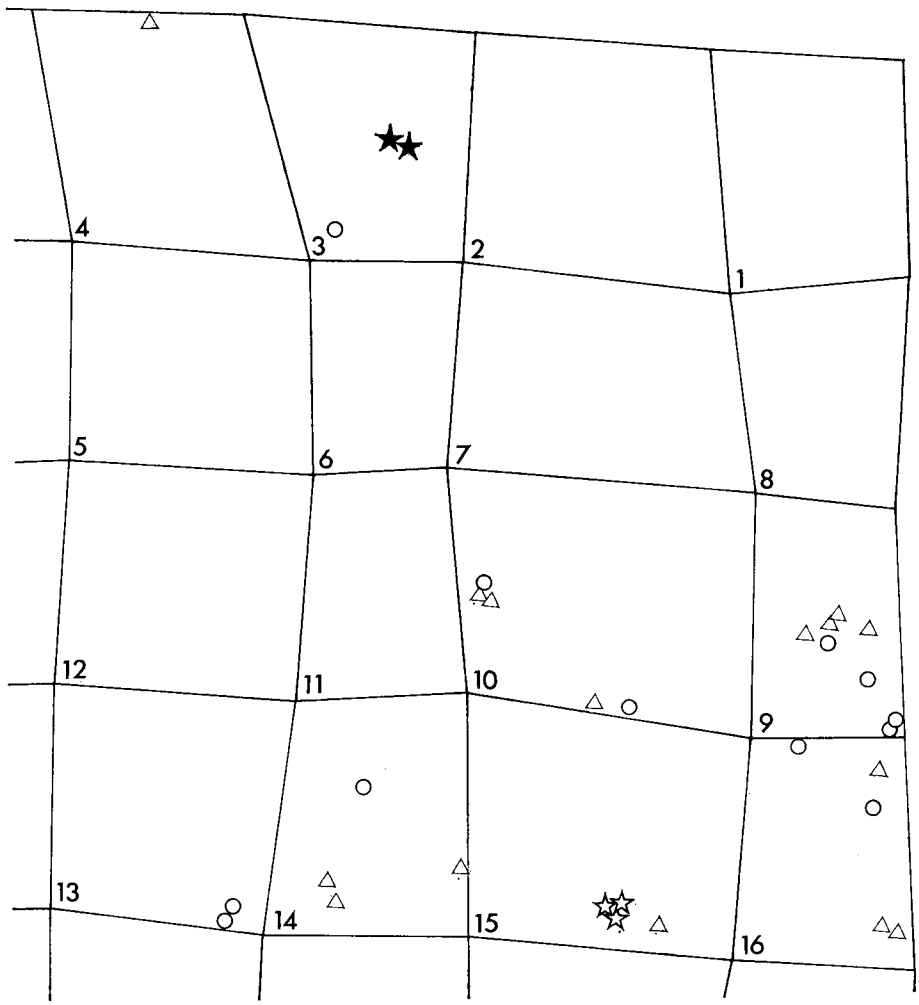


Fig. 16. The spatial position of each karyotype in a part of Gajabuih plot. Open triangle, JJ type; open circle, JV; solid star, JVV of triploid; open star, JJJ of triploid.

affect neither their viability nor propagation behavior.

Some subplots contain high complexity of each type, while others do not (Fig. 17). From the topographical viewpoint, this plot consists of some microenvironmentally different patches, such as a relatively mesic soil on ridges vs. humid soil in dales. Canopies of tree causes dissimilarity in relative light intensity at the forest floor. Under these conditions individuals are distributed densely at favorable places, but sparsely at unfavorable places (Fig. 15). These microenvironmental variations, however, do not seem to affect the viability and reproduction capability. The comparison of the ratios of the above mentioned karyological characters between the classes from densely growing subplots (maximum; 32 individuals per ca. 100 m^2) to poor ones (minimum; 1 individual) shows no significant difference (Table 9). These results cor-

Table 7. Cytologically observed clone numbers identified by distributing aspects, karyotype and leaf characters at Gajabuih, Pinang Pinang, Pinang Pinang Atas and Airsirah plots

Sites	JJ	JV	VV	Other	3x	Total
Gajabuih pl.	145	114	19		2	280
Pinang Pinang pl.	61	51	4	2		118
Pinang Pinang Atas pl.	28	34	2	1		65
Airsirah pl.	6	9	0		1	16

Table 8. The chi square test on the correlation between plant size and ratio of each satellite chromosome type (A), and B-chromosome (B) at Gajabuih plot. Plant size is expressed by either stem diameter or number of individuals within a clones ("II" and "III"). Triploids are excluded. Numbers in column show observed values and numbers within brackets, expected values.

A. Satellite chromosome

Diameters or ind. no. of clones	Satellite chromosome		Total
	J	V	
2– 4 mm	81 (82.8)	33 (31.2)	114
5– 7	131 (132.2)	51 (49.8)	182
8–10	65 (61.0)	19 (23.0)	84
11–22	28 (29.1)	12 (10.9)	40
II–ind.	67 (68.3)	27 (25.7)	94
III–ind.	32 (30.5)	10 (11.5)	42
Total	404	152	556

Calculated chi square value is 1.6299.
Corresponding probability is 0.898.
The difference is not significant $P>0.05$

B. B-chromosome

Diameters or ind. no. of clones	B-chromosome		Total
	B+	B−	
2– 4 mm	14 (19.5)	44 (38.5)	58
5– 7	39 (31.2)	54 (61.8)	93
8–10	16 (15.1)	29 (29.9)	45
11–22	6 (6.0)	12 (12.0)	18
II–ind.	11 (14.4)	32 (28.6)	43
III–ind.	8 (7.7)	15 (15.3)	23
Total	94	186	280

Calculated chi square value is 6.5578.
Corresponding probability is 0.2557.
The difference is not significant $P>0.05$

respond to the correlation between the ratio of each karyological characters and plant size (Table 8). This suggests that all individuals, irrespective of their charac-

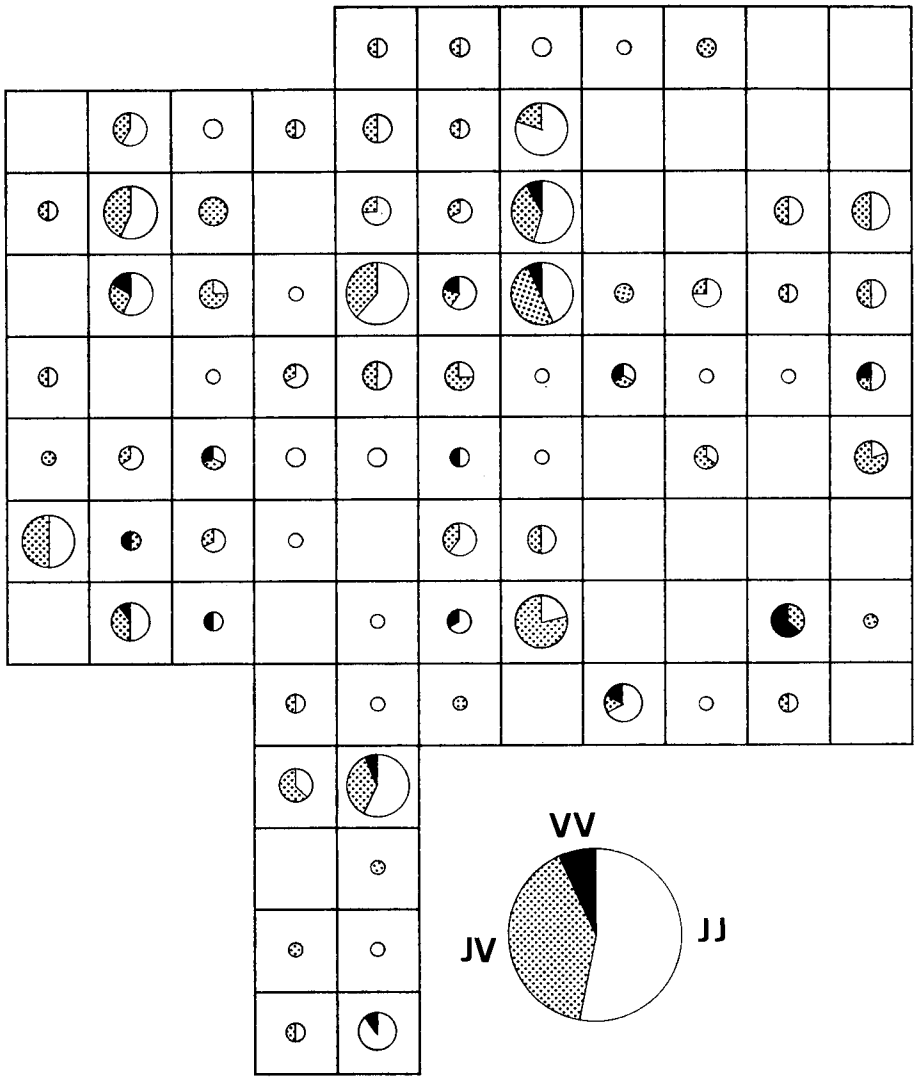


Fig. 17. Circle diagrams showing the ratio of each karyotype at subplots of Gajabuih plot. Size of circles correspond to sample size. Open solid, JJ type; spotted solid, JV; close solid, VV.

teristics, can survive under any environmental condition as far as these conditions remain within the marginal limits of growth. Many neighboring subplots show different proportions of karyological characteristics. Dispersal area of offsprings from few parents (family size) might give rise to these differences. Breeding population area may be more or less 10×10 m^2.

For the exclusion of the difference caused by the above mentioned factors or insufficient sample size at some subplots, subplots were put together to form reasonable group size. Gajabuih plot is divided into six areas based on the empty zones in the

Table 9. The chi square test of the correlation between karyological characters and environments at Gajabuih plot based on individual numbers (excluded triploid). Environmental gradient is expressed by individual numbers of subplots. Numbers in bracket are expected value.

(A) Satellite chromosome type and environment

Environment	J	V	Total
1– 3 ind.	74 (76.3)	28 (25.7)	102
4– 5	78 (77.8)	26 (26.2)	104
6– 7	70 (76.3)	32 (25.7)	102
8–11	91 (88.3)	27 (29.7)	118
12–17	79 (79.3)	27 (26.7)	106
22–32	114 (107.8)	30 (36.2)	144
Total	506	170	676

Calculated chi square value is 4.1402.
Corresponding probability is 0.5294.
The difference is not significant, $P>0.05$.

(B) Homo- vs. heterogeneous sets of satellite chromosome type and environment

Environment	Homo	Hetero	Total
1– 3 ind.	33 (31.7)	18 (19.3)	51
4– 5	32 (32.3)	20 (19.7)	52
6– 7	31 (31.7)	20 (19.3)	51
8–11	38 (36.7)	21 (22.3)	59
12–17	28 (32.9)	25 (20.1)	53
22–32	48 (44.7)	24 (27.3)	72
Total	210	128	338

Calculated chi square value is 2.8988.
Corresponding probability is 0.7156.
The difference is not significant, $P>0.05$.

(C) B-chromosome and environments

Environment	B+	B–	Total
1– 3 ind.	17 (17.3)	36 (35.7)	53
4– 5	20 (18.0)	35 (37.0)	55
6– 7	21 (16.7)	30 (34.3)	51
8–11	21 (19.3)	38 (39.7)	59
12–17	16 (17.3)	37 (35.7)	53
22–32	17 (23.5)	55 (48.5)	72
Total	112	231	343

Calculated chi square value is 5.0923.
Corresponding probability is 0.4047.
The difference is not significant, $P>0.05$.

dales (Fig. 18). Each area includes 33 to 96 clones. Chi square test indicates that the difference of J vs. V type ratio among areas is not sufficiently recognizable. In other words, each type spreads by equal frequency in this plot, although the variations of microenvironment are recognized as mentioned above. The polymorphism in

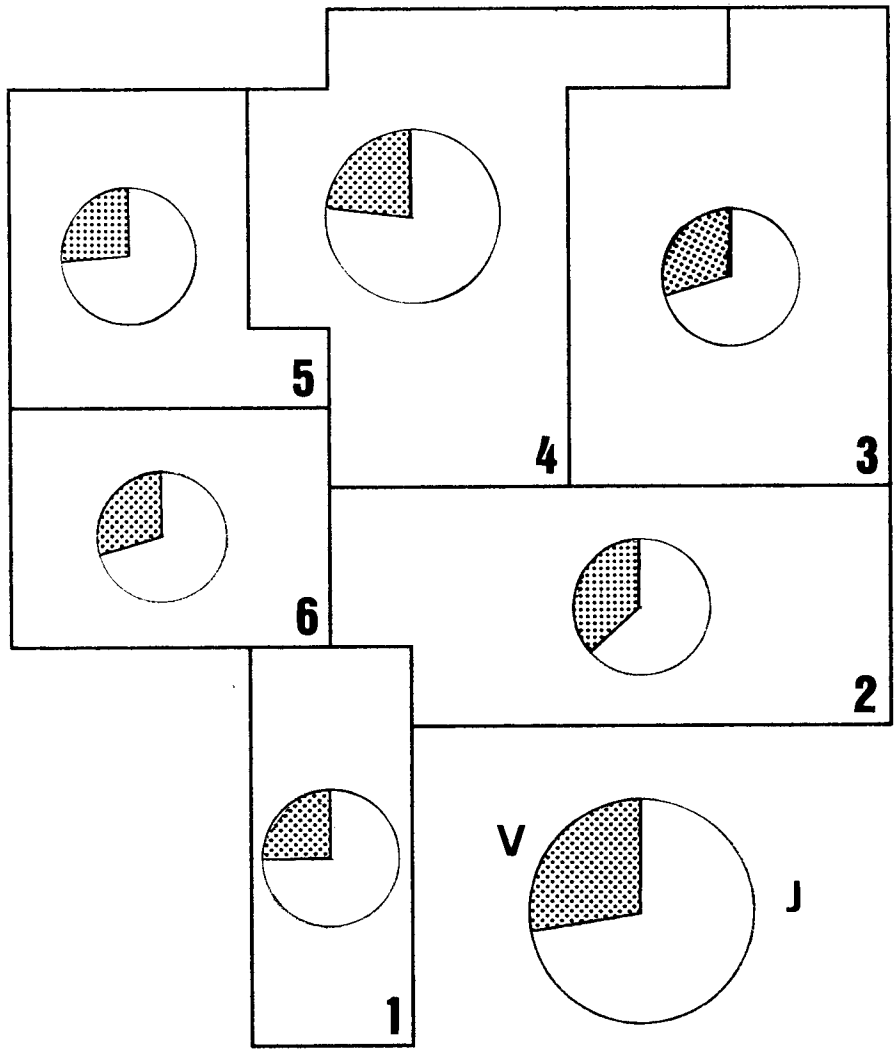


Fig. 18. Proportions of J vs. V type at subdivided areas of Gajabuih plot. Open solid, J; spotted solid, V. Numbers at the lower right corner correspond to A-F of Table 6D.

satellite chromosomes may have little effect on endurance of the so-called selection pressure, or no genetic variation correlates with the chromosomal polymorphism. The same results were obtained from the observations of B-chromosomes (Fig. 19). The statistical analysis of the relation between B-chromosome proportion and plant size or environmental gradient proves no significant differences. While each subplot varies in the ratio of B-chromosomes, for example, none of the clones in subplots No. 78, 85 and 95 possess B-chromosomes, while at subplots No. 34 and 62 all possess B-chromosomes. Moreover, graded degrees from low to high ratio of B-chromosomes are observed. Either random genetic drift acts upon the difference of proportion of B-

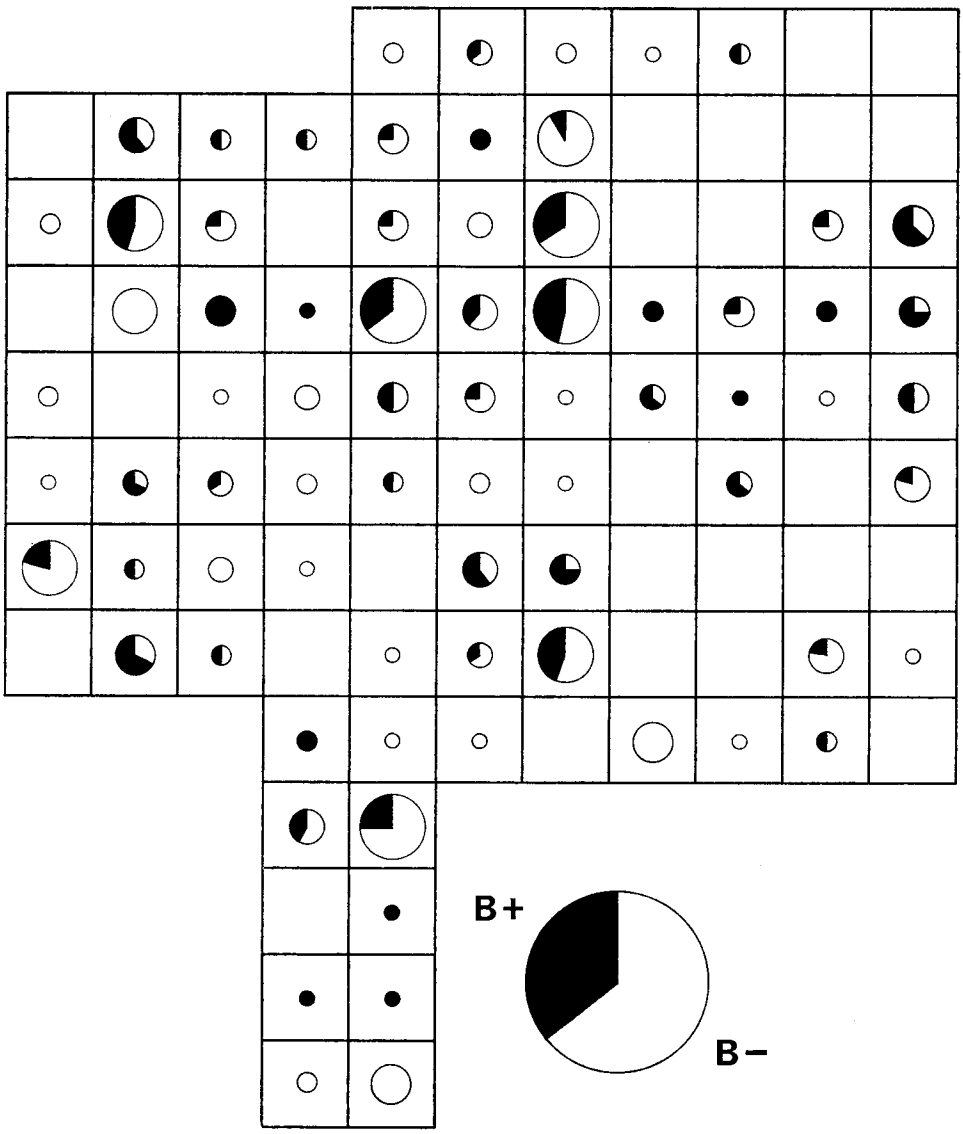


Fig. 19. Circle diagrams showing the ratio of B-containing clones at subplots of Gajabuih plot. Size of circles correspond to sample size. Black solid, with B-chromosomes; open solid, without B-chromosome.

chromosome among subplots, or the size of offspring dispersal is reflected in this aspect. Chi square test is also applied for the analysis of partial difference between these areas. The result suggests no significant differences between subdivided areas.

B. Pinang Pinang plot

The karyotype of 138 individuals of this plot were observed and they are divide into 118 clones (Table 7). Two peculiar mutants on the satellite chromosomes were found at the point beside limestone area. Two individuals (one clone) at subplot

No. 70 possess the third type satellite chromosomes, while 2 of 10 individuals (one clone) of subplot No. 35 have the fourth type. They propagate vegetatively and these mutants show the same range of variation in leaf characters or growth condition as those of the others. The karyological data at this plot are insufficient for detailed analysis.

C. Pinang Pinang Atas plot

In this plot, the karyotype of 66 of 72 clones were observed (Table 7). One of the mutations on satellite chromosome, the fifth type, was found in this plot. There is no significant difference in the distribution pattern of satellite chromosome and B-containing clones. Almost all aspects of the karyotype variation of this plot are the same as those of the populations of Gajabuih and Pinang Pinang plots.

D. Airsirah plot

In this plot four triploid individuals (one clone) were found at subplot No. 7, the chromosome complement of which consists of JJJ type but without B-chromosome. The neighboring clone possesses JJ set, but not B-chromosome. Both clones are phenotypically practically the same, which suggests that this triploid clone originated from the diploid clone at that place.

In contrast with the other two plots, majority of the clones (9 out of 16) possess JV type (Table 7). VV type is not found in this plot. The frequency of clones with B-chromosome is very low, only 2 out of 13.

5. Changes of Population in 1982–1984

Two years after the collection of the upper part of the stem of all individuals, we re-examined the area to know what characters are dominant in the new population (established mainly by seeds) at a part of Pinang Pinang plot (Fig. 20). Both the original and the new population occurred approximately in the same clone numbers, i.e., 200 vs. 167, respectively. It means that this species rapidly recovered its ecological position. Whether the renewed population shows some different from the old ones is very interesting for the determination of the selection pressure against the characters observed act on the seedling's survival. The former contained both single and plural clones, while the latter mainly single clones growing up from seedlings. Chi square test suggests that neither there is no significant difference between the original and the renewed one, nor the dead or surviving clones concerned with phenotypic variations (Fig. 21, Table 10). No selection pressure may act on the viability of any of the characters from seedling to mature stage. On the other hand, there is a tendency that in subplots with previous dense population rich individuals appear constantly, while individuals in those with less dense population still remain poor. Certain environmental gradient acts toward the viability of this species.

6. Spatial Distribution

Spatial distribution pattern is an important factor for analysis of population structure. Some species grow closely together with other individuals, and sometimes make up colonies or clumps. On the other hand, some grow alone and exclusively from other individuals. The spatial distribution pattern contains many informations

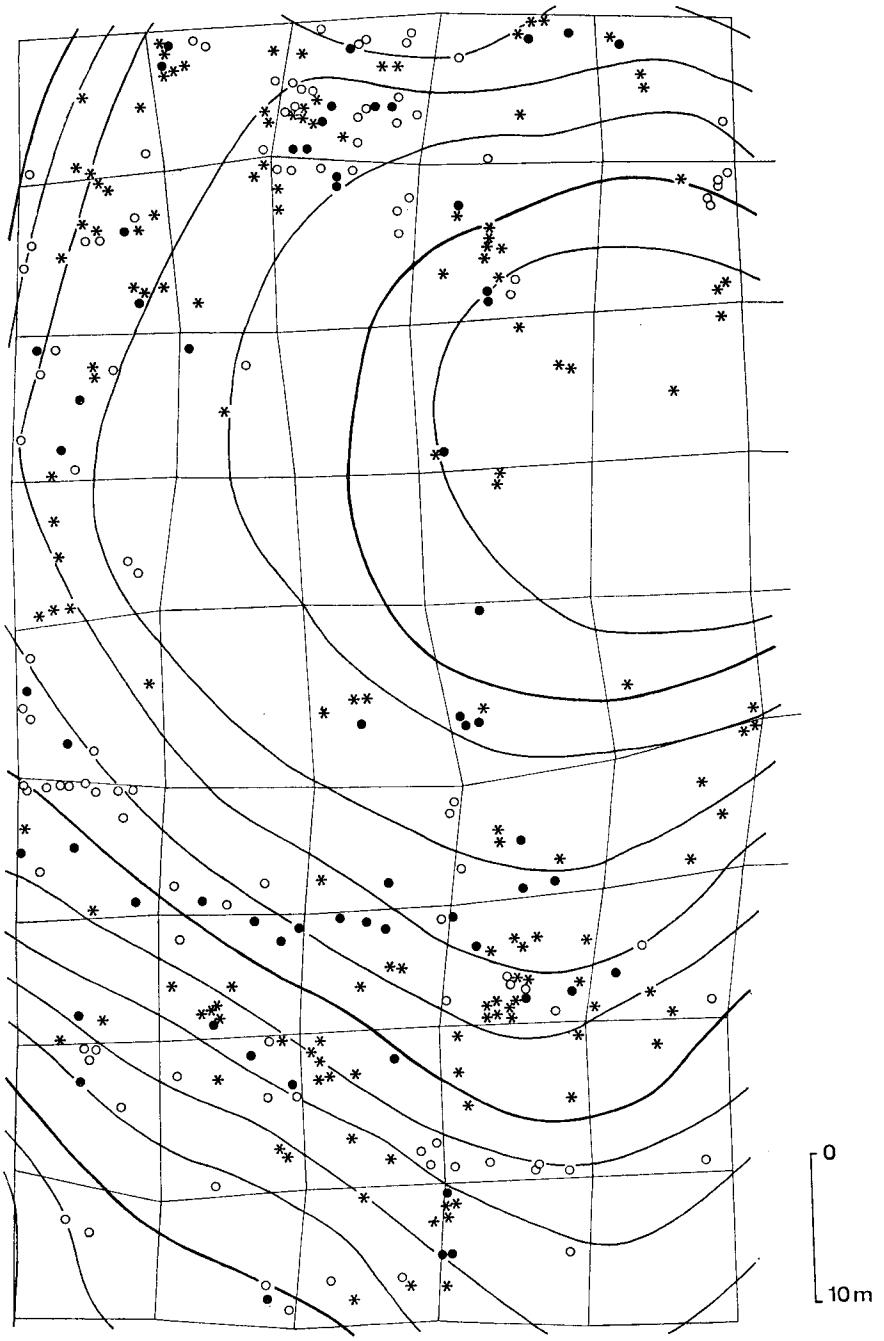


Fig. 20. The map of spatial positions of clones at renewed population corresponding to subplots no. 1–45 of Pinang Pinang plot. Asterisk, dead; solid circle, survival; open circle, renew.

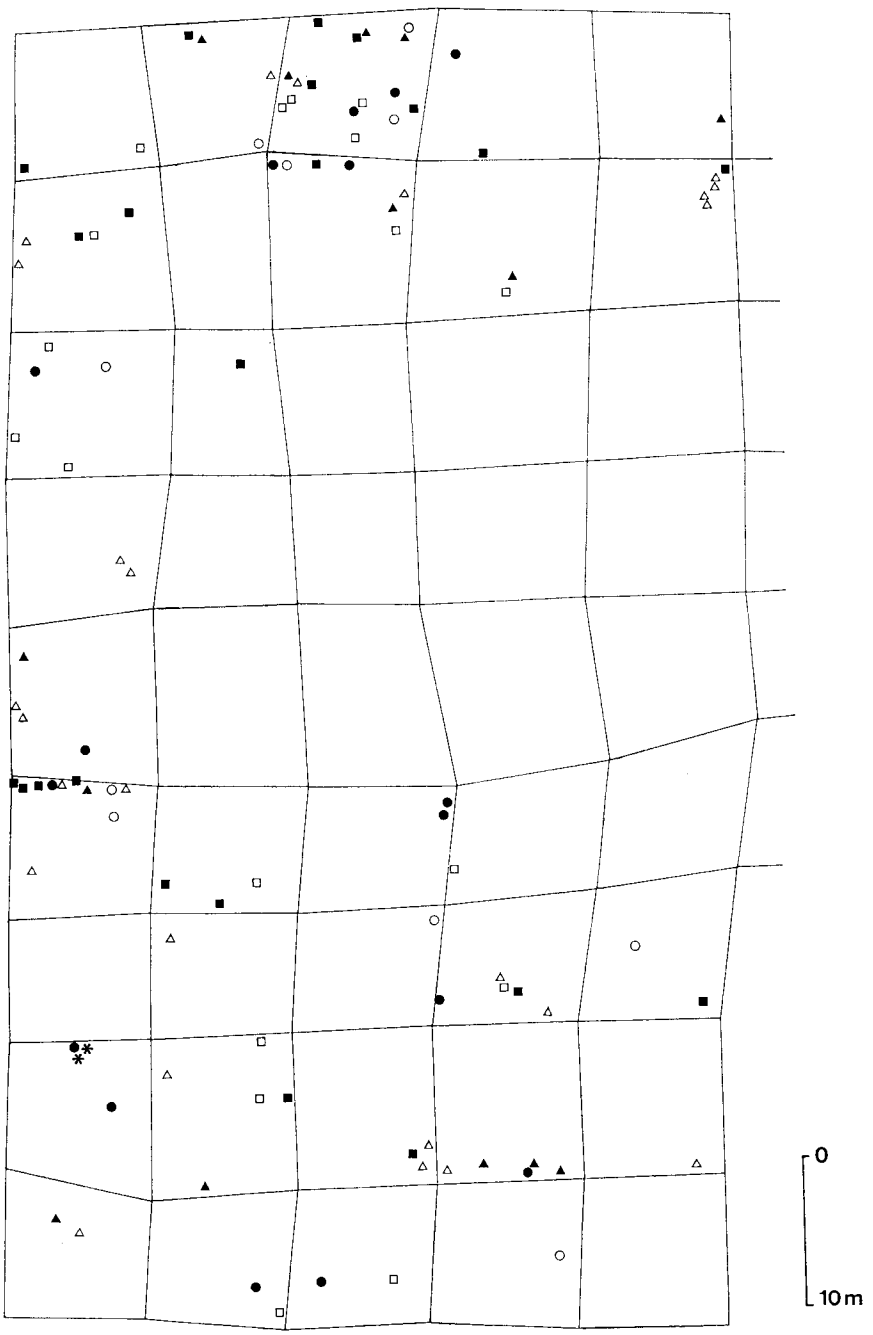


Fig. 21. The map of spatial positions of growing clones at renewed population corresponding to subplot No. 1–45 of Pinang Pinang plot showing leaf characters. Solid circle, GGG; open circle, GGW; asterisk, GRG; solid square, RGG; open square, RGW; solid triangle, RRG; open triangle, RRW. (cf. Table 10).

Table 10. Leaf character and karyotype of clones at renewed population of Pinang Pinang.

	No.	Leaf								Karyotype				
		PC		LC		MOT				B+	B−	JJ	JV	VV
		G	R	G	R	G	W1	W2	W3					
Dead	140	40	100	99	41	62	56	15	7	11	18	17	11	1
Surv.	60	16	44	41	19	27	13	17	3	3	11	7	6	1
Renew	107	28	79	66	41	54	19	29	5	—	—	—	—	—

The chi square test of leaf characters.
Numbers in brackets are expected values.

A. Petiole color

	G	R	Total
Dead	40 (38.3)	100 (101.7)	140
Surv.	16 (16.4)	44 (43.6)	60
Renew	28 (29.3)	79 (77.7)	107
Total	84	223	307

Calculated chi square value is 0.1944.
Corresponding probability is 0.9074.
The difference is not significant $P>0.05$.

B. Leaf color

	G	R	Total
Dead	99 (93.9)	41 (46.1)	140
Surv.	41 (40.3)	19 (19.7)	60
Renew	66 (71.8)	41 (35.2)	107
Total	206	101	307

Calculated chi square value is 2.2925.
Corresponding probability is 0.3178.
The difference is not significant $P>0.05$.

C. Leaf mottle

	G	W	Total
Dead	62 (65.2)	78 (74.8)	140
Surv.	27 (27.9)	33 (32.1)	60
Renew	54 (49.8)	53 (57.2)	107
Total	143	164	307

Calculated chi square value is 1.0061.
Corresponding probability is 0.6047.
The difference is not significant $P>0.05$.

D. Combination of petiole color and leaf color

	GG	RG	RR	Total
Dead	40 (37.3)	59 (57.6)	41 (45.1)	140
Surv.	15 (15.7)	26 (24.3)	18 (19.0)	59*
Renew	26 (28.0)	40 (43.2)	39 (33.8)	105*
Total	81	125	98	304*

*: minor element of "GR" is excluded.
Calculated chi square value is 1.9786.
Corresponding probability is 0.7397.
The difference is not significant $P>0.05$.

(cont'd.)

(Table 10. cont'd.)

The chi square test of karyotypes.
Numbers enclosed by bracket are expected values.

A. Satellite chromosome

	J	V	Total
Dead	45 (43.8)	13 (14.2)	58
Surv.	20 (21.2)	8 (6.8)	28
Total	65	21	86

Calculated value of chi square is 0.3880.
Probability of correlation is 0.5334.
The difference is not significant $P>0.05$.

B. B-chromosome

Fisher's exact probability test of B-chromosome ratio between dead and survival clones at Pinang Pinang plot.

	B+	B−	Total
Dead	11	18	29
Surv.	3	11	14

Corresponding probability is 0.4681.
The difference is not significant $P>0.05$.

of species peculiarity, but data on the population structure is still few. Recently Huenneke (1985) reported the spatial distribution of genetic individuals within *Alnus incana* ssp. *rugosa*, and discussed the genetic structure of population.

Spatial distribution pattern is analyzed by $\overset{*}{m}$-m method which may clarify the internal structure based on the relation between mean crowding, $\overset{*}{m}$ and mean density, m (Iwao 1972). It applies to a part of both Gajabuih and Pinang Pinang plots using successive change of the quadrat size to detect the infra-population structure. The area at Gajabuih is 60×60 m^2 and 40×80 m^2 at Pinang Pinang plot (Fig. 22). Figures 23A and 23B show the $\overset{*}{m}$-m relation on both plots and suggest the existence of clumps.

Further analysis of the clump or patch structure and their distribution pattern are carried out by Iwao's (1972) ρ- and τ-indexes (Fig. 24). In both cases of using either individuals or clones as a basic unit for this analysis, ρ- and τ-graph show two peaks, which indicate the existence of double clump structure in Gajabuih plot. The features of Pinang Pinang plot are a little different from Gajabuih plot. In the case of using of individuals only one low peak appeared, which indicates a loose single clump st ucture. While, clones construct double clump structure like that in Gajabuih plot. In Pinang Pinang plot the vegetative reproduction make the clump structure unclear. The area of the smaller clump is estimated to be about 0.75 m^2 in Gajabuih plot and 1.6 m^2 in Pinang Pinang plot (Fig. 24), which correspond to the size of offspring dispersal. The large clump is looser than small one and occupies approximately 56–100 m^2. This area corresponds to a maximum biased patch size which will be discussed latter. According to Iwao's simulation (1972), these graphs also suggest that these clumps are

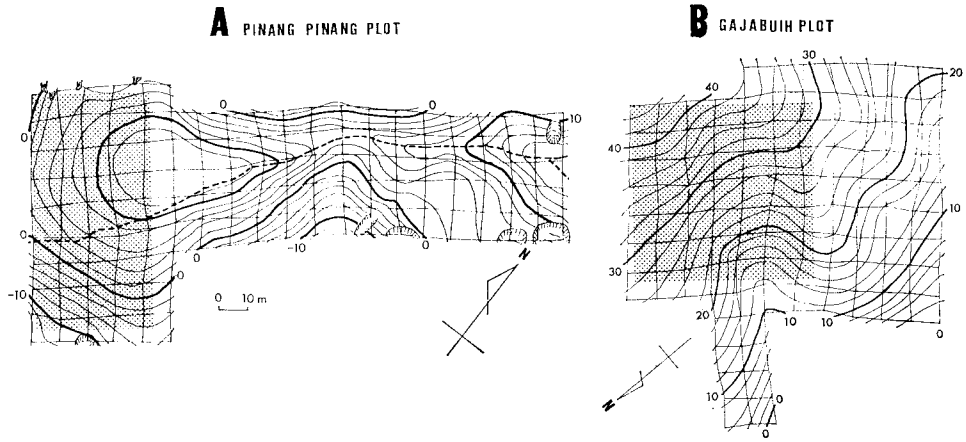


Fig. 22. Topographical maps of Pinang Pinang (A) and Gajabuih (B) plots. Individuals at dotted areas are analyzed by $\overset{*}{m}$-m method. Measured and drown by Dr. K. Ogino, 1981.

distributed in a rather aggressive pattern.

Spatial arrangement of each phenotype is analyzed based on the relations between inter-phenotype mean crowding ($\overset{*}{m}$) and mean density (m). This method was originated by Iwao (1977) to analyze the pattern of association between two alleles. Two indexes were proposed; the γ index indicates the degree of overlapping, which takes the maximum value of 1 when both species are distributed completely overlapping, while the minimum value 0 arises from the mutually exclusive distribution. The second index ω expresses the degree of spatial correlation or the degree of overlapping in relation with the independent distributions. The maximum value of 1 indicates complete overlapping distribution pattern, the value 0 independent, and minimum value of -1 complete exclusion, while intermediate values suggest gradual conditions.

The $\overset{*}{m}$-m relation between two phenotypes, for example, between plants with green and red color leaf in Gajabuih plot is shown in Figure 25. The low value of index γ at the points less than 1/128 (ca. 30 m^2) of quadrat size suggests that individuals or clones of each phenotype are distributed rather excursively. The aspect turns over abruptly at the point of about 1/128–1/64 (ca. 56 m^2). The γ index rapidly approaches value of 1. On the other hand, index ω takes a large value above these quadrat size. These results suggest that the relation between inter-phenotypes are overlapping in these quadrat sizes. It further suggests that in quadrat larger than 1/64, each subdivision of population becomes rather homogeneous in their ratio of leaf phenotypes.

The analysis of mottle type in this plot and of both characters in Pinang Pinang plot showed similarity. From these results, it is concluded that about 100 m^2 can be called maximum biased patch size in which the ratio of each genetical character fluctuates by random drift and/or by sib mating. In broader area, their ratio become uniform.

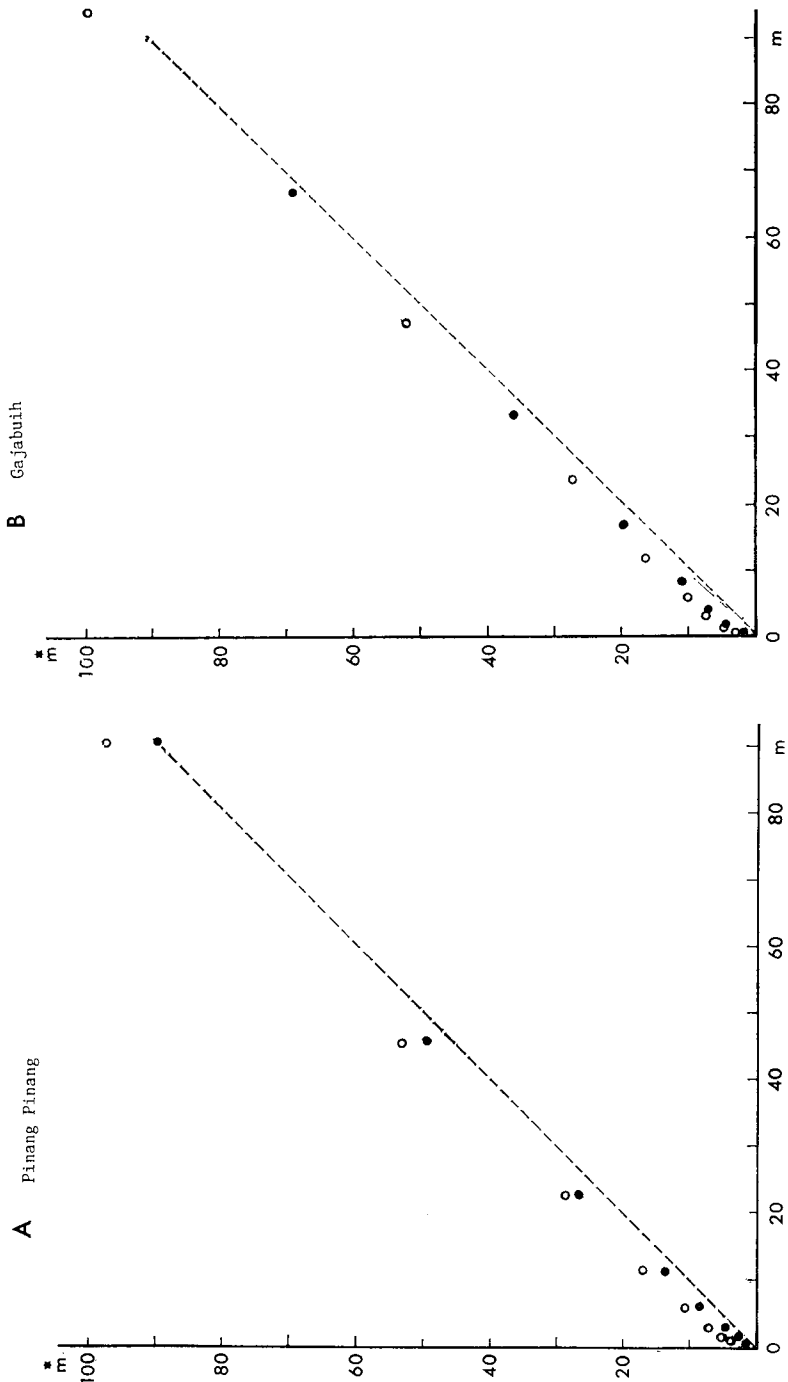


Fig. 23. The m*-m relations by successive changes of quadrat size. A, Pinang Pinang plot; B, Gajabuih plot. Open circle, taking basic unit as individual; closed circle, taking basic unit as clone; broken line, $m^* = m$.

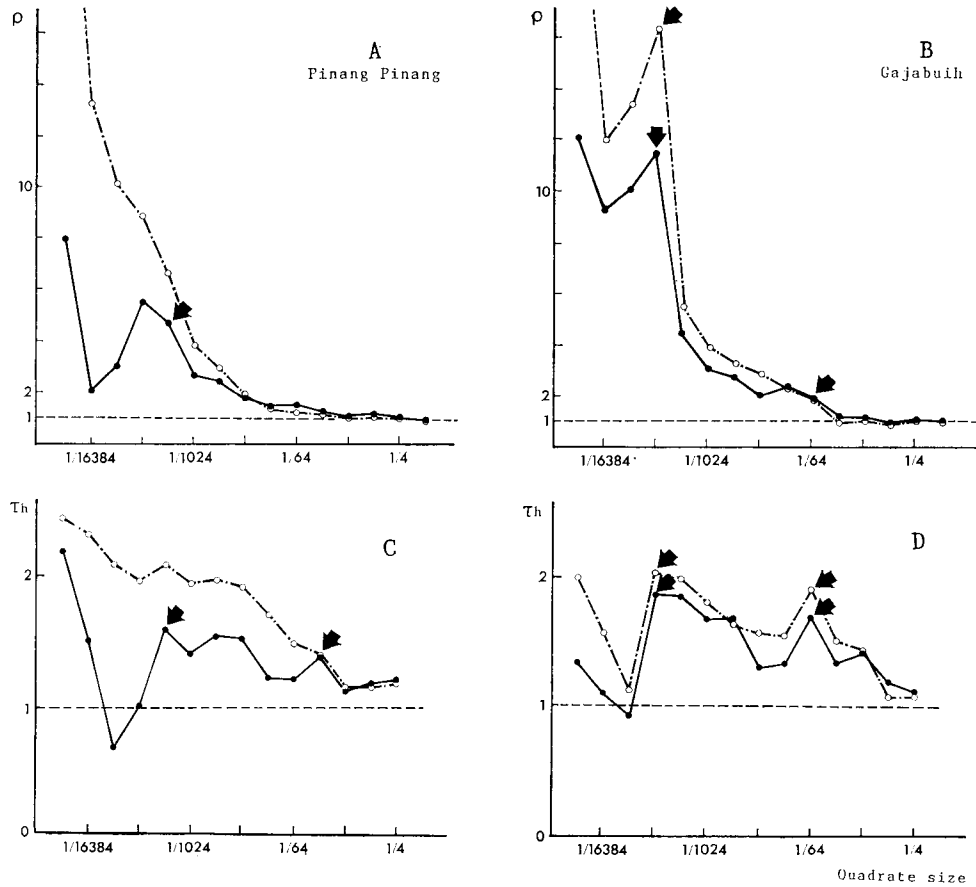


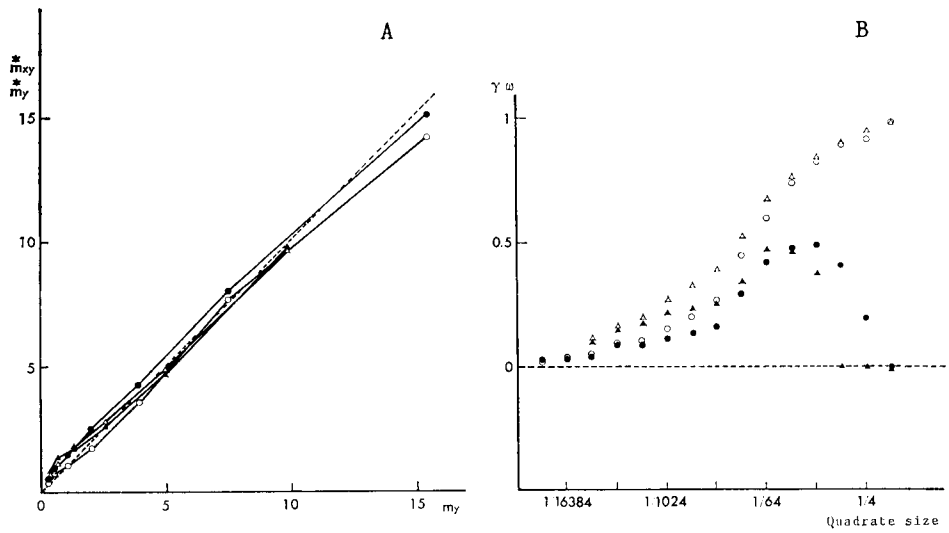
Fig. 24. The graph of ρ- and τ-index with successive change of quadrat size. A, ρ graph of Pinang Pinang plot; B, ρ graph of Gajabuih plot; C, τ graph of Pinang Pinang plot; D: τ graph of Gajabuih plot. Open circle, taking basic unit as individual; closed circle, taking basic unit as clone. Arrows indicate existence of clump.

V. Variation in Local Population

When sampling was done in areas other than these plots, we sampled the plants of compact colony as a basic unit of local population, which is called a site here. The area of sites varies from 5 to 100 m^2. Even in such a small colony, we can find several phenotype combinations (Plate I-A). When several sites are put together in a higher level of population and are separated topographically and ecologically, we call them a location. The variation patterns of the proportion of each character are examined in both levels to elucidate the population structure and diversity of this species.

1. Correspondence between Values Calculated from Individual and Clone Numbers

Recognition of individuality is a prerequisite for understanding the population structure of plants with vegetative reproduction system. The ratio of both phenotypical



F g. 25. A: $\overset{*}{m}$-m relation of inter- and intraphenotypes of leaf undersurface color in Gajabuih plot. m_y, mean of red undersurface plants; $\overset{*}{m}_y$, mean crowdings of red; $\overset{*}{m}_{xy}$, mean crowdings of green for red; open circle, $\overset{*}{m}_y$ of clone; filled circle, $\overset{*}{m}_{xy}$ of clone; open triangle, $\overset{*}{m}_y$ of individual; filled triangle, $\overset{*}{m}_{xy}$ of individual.: γ and ω index with successive changing of quadrat size. Open circle, γ index of clone; filled circle, ω index of clone; open triangle, γ index of individual; filled triangle, ω index of individual. Explanation in text.

and karyological characteristics calculated from individuals might not represent the real frequency of the population. The biggest clone at subplot No. 95 of Gajabuih plot with 14 individuals has to be equivalent to 1 clone, for example. It is impossible to identify the clones of samples from zones other than plots, for no record of their spatial positions is available. The values based on individuals exactly correspond to those on clones is checked by examining the sample from Gajabuih plot population. Plants of all size class of both single and plural clones possess similar proportion of leaf color, leaf mottle, satellite chromosomes and B-chromosomes (Figs. 13, 14, Tables 8A, B, 11, 12). The values obtained from clones are directly comparable with those from individuals.

2. Ratio of Leaf Color and Mottle

The ratio of the leaf characters in each site varied widely. Figures 26A and 26B show an example of variation in leaf color and mottle in the sites along one ridge from low (550 m) to high (1100 m) altitude. Some phenotypes do not exist in both small and rather large sites. (red color in BA-1, BC-2). Extreme variations of the ratio of phenotype among sites are considered to be caused by small sampling size and/or founder effect. On higher level, location, the variations in leaf color and leaf mottle are different (Fig. 27). The ratio of leaf color varies in widely too. GG location shows extremely different proportion of leaf color from KM location situated close to

Table 11. Chi square test of leaf color types in two plots, Pinang Pinang (A) and Gajabuih (B), based on individuals and clones respectively. Numbers in brackets are expected values.

A. *Pinang Pinang plot.*

	GG	GR	RG	RR	Total
Clone	137 (140.8)	3 (*)	188 (188.8)	154 (149.4)	482
Ind.	239 (235.2)	4 (*)	316 (315.2)	245 (249.6)	804

Calculated chi square value is 0.3936.
Corresponding probability is 0.8214.
The difference is not significant $P>0.05$.

* Omitting for chi square test because of its small expected value.

B. *Gajabuih plot.*

	GG	GR	RG	RR	Total
Clone	98 (95.8)	1 (*)	158 (160.4)	64 (63.8)	321
Ind.	133 (135.2)	1 (*)	229 (226.6)	90 (90.2)	453

Calculated chi square value is 0.1530.
Corresponding probability is 0.9264.
The difference is not significant $P>0.05$.

* Omitting for chi square test because of its small expected value.

Table 12. Chi square test of leaf mottle types in two plots, Pinang Pinang (A) and Gajabuih (B), based on individuals and clones respectively. Numbers in bracket are expected values.

A. *Pinang Pinang plot.*

	G	W1	W2	W3	Total
Clone	204 (199.6)	181 (188.7)	85 (80.3)	12 (13.5)	482
Ind.	328 (332.4)	322 (314.3)	129 (133.7)	24 (22.5)	803

Calculated chi square value is 1.3719.
Corresponding probability is 0.7121.
The difference is not significant $P>0.05$.

B. *Gajabuih plot.*

	G	W1	W2	W3	Total
Clone	183 (184.9)	83 (84.8)	43 (41.5)	13 (10.8)	322
Ind.	262 (260.1)	121 (119.2)	57 (58.5)	13 (15.2)	453

Calculated chi square value is 0.9470.
Corresponding probability is 0.8141.
The difference is not significant $P>0.05$.

GG and under similar environment. This extreme variation may give rise to extreme situation. The ratio of mottle leaf remains rather constant (about 60%), except in GG location which is one of the highest and marginal population of this species. It seems to be caused by a constant gene flow among locations. However, contradictory factors such variable ratios of leaf color between close locations and the pollinator's behavior of this species reduce this possibility. In any way, the variation of the ratio of each phenotype is not associated with altitude.

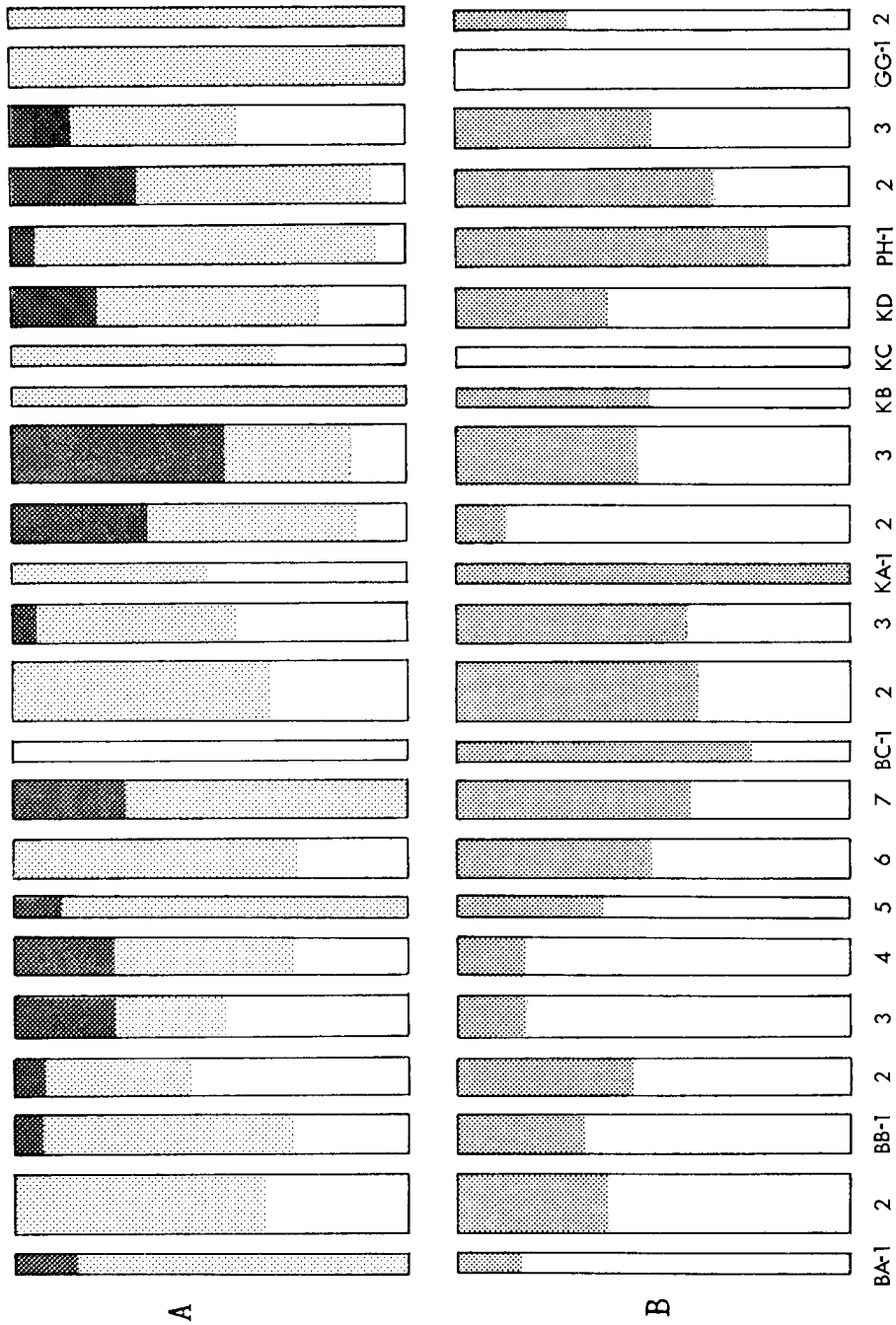


Fig. 26. Ratio of leaf phenotype in sites along the ridge of Mt. Gadut. A, combinations of color of petiole and leaf undersurface. Open, GG; sparsely dotted, RG; densely dotted, RR. B: leaf mottle. Open, without mottle (G); dotted, with mottle (W1–W3). Symbols correspond to Table 1. Width of diagram corresponds to three classes of sample size as less than 9 individuals, 10 to 19 indivduals and more than 20 individuals.

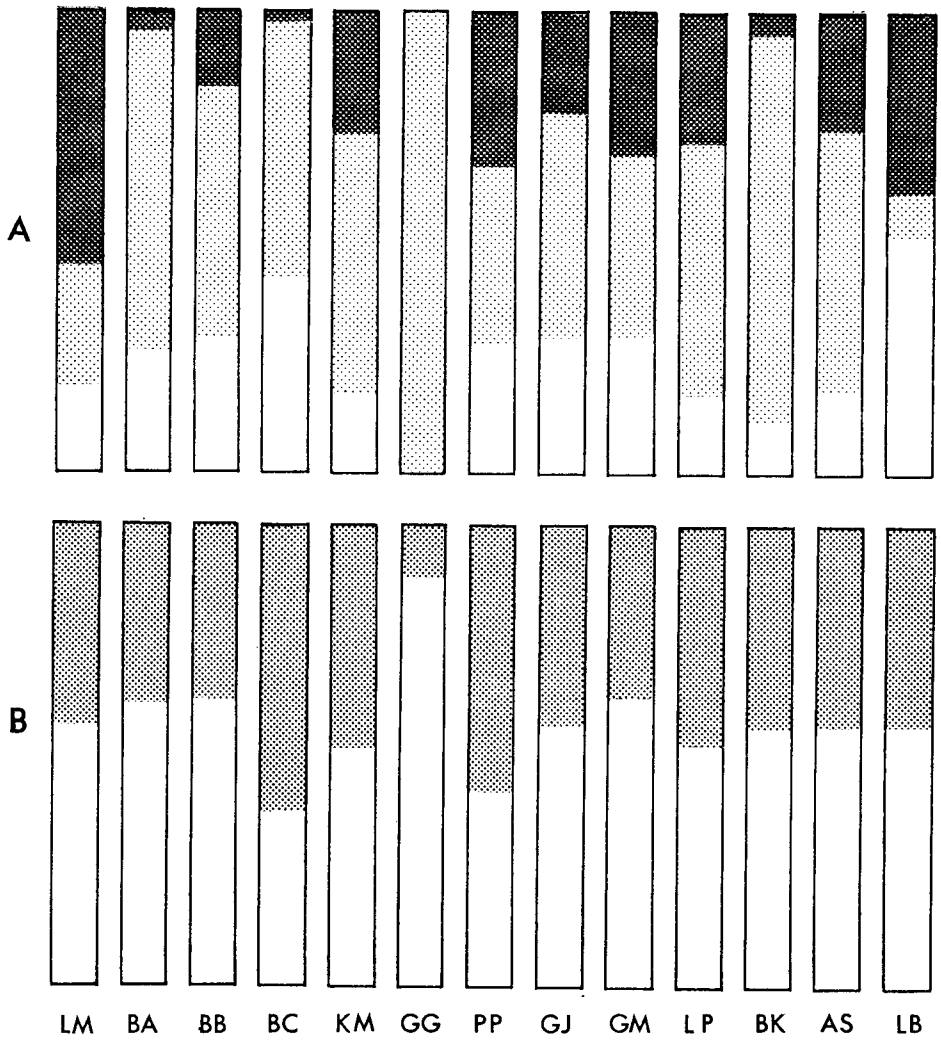


Fig. 27. Ratio of leaf phenotype in locations. A, color of petiole and leaf undersurface. Open, GG; sparsely dotted, RG; densely dotted, RR. B, leaf mottle. Open, without mottle (G); dotted, with mottle (W1–W3). Symbols correspond to Table 2.

3. Ratio of Satellite Chromosome Type

Total sum of J or V type satellite chromosome in each population is, at first, calculated for statistic analysis. The complement of satellite chromosome in Gajabuih plot is estimated as follows. Individuals with JJ have 2 J type, those with JV have 1 J and 1 V, and those with VV have 2 V, therefore the population of Gajabuih plot keeps $189\times2+128=506$J and $21\times2+128=170$V. These numbers express one of the gene components concerned with the position of the nucleolar organizing locus. In all populations except Lurah Berangin population the ratio of J type occupies more or less

two third (Figs. 28A, 30, Table 13). The Fisher's exact probability test proves that there are no significant differences between populations, with the exception of Lurah Berangin population (Table 14). The possible explanation why the latter population has no V type is not yet known.

Airsirah plot and Gn. Gadut populations are located at about the highest margin of growth of this species, i.e. about 1100 meters above sea level, while Bt. Gajabuih and Bt. Pinang Pinang are probably the most favorable areas for this species judging from the growth density of individuals (25/1000 m^2 vs. 456 or 805/10000 m^2). The fact that almost all kinds of mutations are observed here supports this idea. It seems, however,

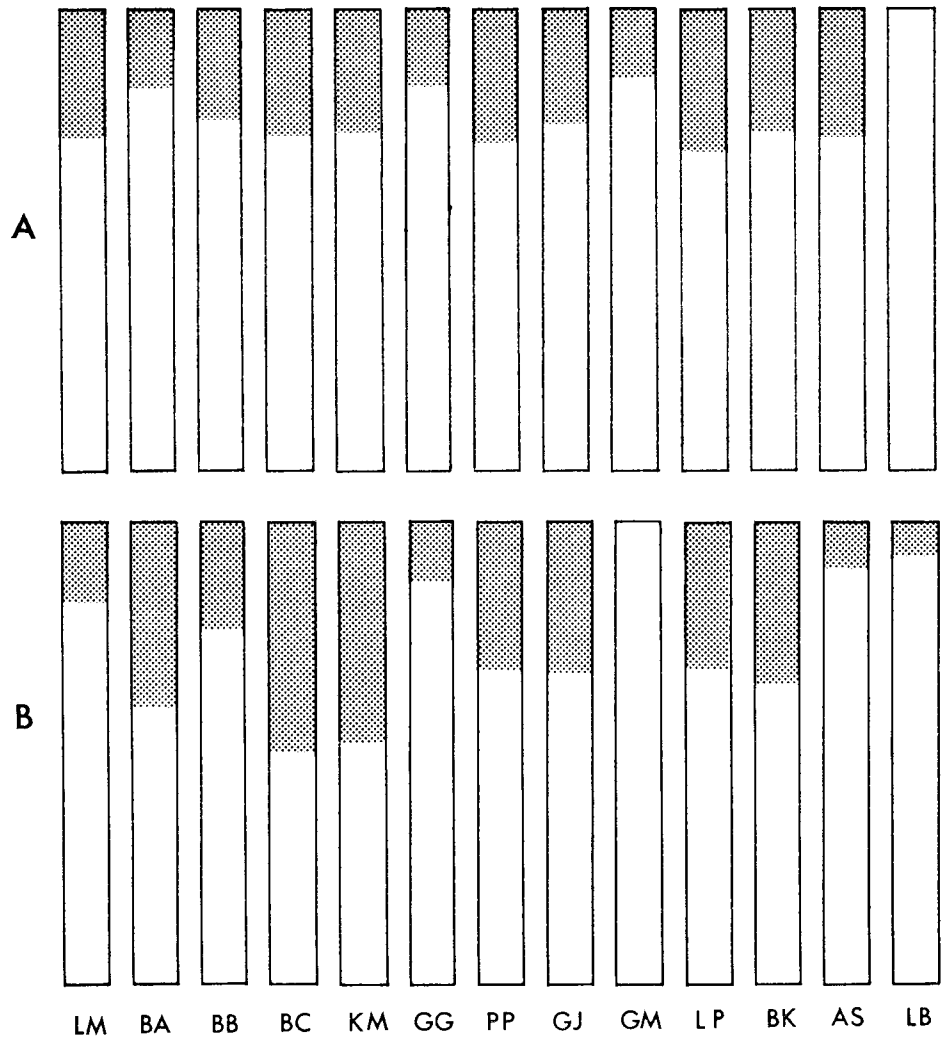


Fig. 28. Ratio of karyological characters in locations. A, satellite chromosome. Open, J; dotted, V. B: B-chromosomes. Open, B-chromosome absent; dotted, present. Symbols correspond to Table 2.

Table 13. The ratio of J and V type satellite chromosome in locations other than Gajabuih and Pinang Pinang plots. Values are caluculated based on individuals. The numbers enclosed by brackets are expected values.

Locations	J	V	Total
Limau Manis	33 (34.0)	13 (12.0)	46
Bali Bukit	25 (22.2)	5 (7.8)	30
Bt. B. B.	65 (63.6)	21 (22.4)	86
Bt. Lantik	49 (50.3)	19 (17.7)	68
Bt. Kambut	41 (41.4)	15 (14.6)	56
Gn. Gadut	25 (22.2)	5 (7.8)	30
Bt. Pinang.	150 (161.1)	68 (56.9)	218
Bt. Gajab.	81 (79.8)	27 (28.2)	108
Bt. Gambir	29 (25.1)	5 (8.9)	34
Ladang Padi	61 (65.0)	27 (23.0)	88
Bt. Karang	29 (29.6)	11 (10.4)	40
Airsirah	23 (23.6)	9 (8.4)	32
Lurah Berang.	26 (19.2)	0 (6.8)	26
Total	637	225	862

Calculated chi square value is 18.6745.
Corresponding probability is 0.0962.
The difference is not significant, $P>0.05$.

that neither adverse nor favorable environments affect neither the viability nor the diversity of phenotypes and karyotypes. When V type mutant occurred, it had more advantageous effect on the viability and dispersal than J type. Otherwise, this type could not spread into almost all populations. Probability of more frequent occurrences of V type from J type mutation may be rejected. The frequent existences of the other types of mutations on satellite chromosome indicate no necessity of consideration that there is some structural liability changing from J to V type. Karyological variation of V and J type is not yet found in another allied species although the other karyological mutation is observed. At the present time, it is considered that selection pressure, however, equilibrates on each type at any populations. Chi square test on the correlation of ratio of each type and plant size (Table 8) is also suggestive to this idea. There is no significant difference in the proportion of J or V chromosome among size classes. If there were some different degree of fitness, some type must be decreased or extinct.

Judging from their minority in populations, other types of chromosomal mutation are relatively new ones. In any case they can not spread widely because they propagate only vegetatively.

For clarification of the sexual reproductive system of each cytotype and how individuals with heterogeneous set conserve certain ratio in any populations, further study of the chromosome behavior at meiotic cell division and fertility of pollen grain or seed sets is required.

4. Ratio of B-chromosome

The ratio of individuals with B-chromosome in each location is shown in Figure 28B and Table 15. Further analysis by Fisher's exact probability test of all populations (Table 16) suggests that Bt. Gambir and some populations differ extremely from the

Table 14. Fisher's exact probability test on the ratio of satellite chromosomes. Values are calculated by two-side test. The values under 0.05 with asterisk "*" or 0.01 with "**" suggest the significant difference between two samples. LM: Limau Manis. BA: Bali Bukit. BB: Bt. Batu Bajolang. BC: Bt. Lantik. KM: Bt. Kambut. GG: Gn. Gadut. PP-1: Pinang Pinang plot. PP: Bt. Pinang Pinang. GJ-1: Gajabuih plot. GJ: Bt. Gajabuih. GM: Bt. Gambir. LP: Ladang Padi. BK: Bt. Karang. AS: Airsirah plot. LB: Lurah Berangin.

	BA	BB	BC	KM	GG	PP-1	PP	GJ-1	GJ	GM	LP	BK	AS	LB
LM	.377	1.51	1.20	1.30	.377	1.34	.841	1.40	1.47	.243	.934	1.13	1.20	.003**
BA	–	.544	.348	.433	1.27	.343	.146	.351	.485	1.10	.205	.438	.440	.075
BB		–	1.50	1.40	.544	.819	.303	.860	1.06	.361	.451	1.45	1.49	.004**
BC			–	1.05	.348	1.32	.728	1.38	1.46	.212	.848	1.14	1.21	.002**
KM				–	.433	1.18	.641	1.24	1.34	.281	.758	1.25	1.31	.003**
GG					–	.343	.146	.351	.485	1.10	.205	.438	.440	.075
PP-1						–	1.79	1.18	.873	.192	1.63	1.27	1.33	.001**
PP							–	1.88	.303	.067	1.04	.793	.900	.000**
GJ-1								–	.923	.193	1.71	1.32	1.38	.001**
GJ									–	.308	1.70	1.41	1.45	.003**
GM										–	.109	.294	.302	.102
LP											–	.884	.976	.001**
BK												–	1.26	.004**
AS													–	.005**

Table 15. Ratio of individuals with vs. without B-chromosomes including triploid and those with minor mutants on karyotype. Numbers in brackets are expected values.

Locations	B+	B−	Total
Limau Manis	4 (7.3)	19 (15.7)	23
Bali Bukit	6 (4.8)	9 (10.2)	15
Bt. B. B.	14 (13.7)	29 (29.3)	43
Bt. Lantik	17 (10.8)	17 (23.2)	34
Bt. Kambut	14 (9.2)	15 (19.8)	29
Gn. Gadut	2 (4.8)	13 (10.2)	15
Pinang. pl.	41 (43.8)	97 (94.2)	138
Bt. Pinang.	37 (35.0)	73 (75.0)	110
Gajabuih pl.	115 (109.0)	228 (234.0)	343
Bt. Gajabuih	18 (17.2)	36 (36.8)	54
Bt. Gambir	0 (5.4)	17 (11.6)	17
Ladang Padi	14 (14.0)	30 (30.0)	44
Bt. Karang	7 (6.4)	13 (13.6)	20
Airsirah pl.	2 (6.4)	18 (13.6)	20
Lurah Berangin	1 (4.4)	13 (9.6)	14
Total	292	627	919

Calculated chi square value is 30.9427. Corresponding probability is 0.0057. The difference is highly significant, $P<0.01$.

others. B-chromosome is not found in them at all (Tables 3, 15). The population of Bt. Gambir is situated at about 600–700 meters elevation from sea level and at mid-slope under the primary forest. Almost all environmental conditions here seem to be the same as those at Bt. Gajabuih which is presumed to be one of the most favorable areas for this species. Airsirah plot, the marginal area, is also composed of a very few B-chromosomes. Therefore, environmental conditions do not seems to be strict factors in the selection pressure of the viability of B-containing individuals. The fact that different cells of the same individual show different B-chromosome distribution (Fig. 8) in this species and also in *Schismatoglottis okadai* (Okada, unpubl.) suggest that B-chromosome has little genetic rule. No significant correlation exists between B-chromosome and plant size as well. So many instances have been reported concerning B-chromosome distribution in natural populations (Jones & Rees, 1982). In some species B-chromosome distribution is directly correlated with environmental gradient, such as humidity and soil. While, Semple (1974) reported phenomenon in *Xanthisma texanum* (Asteraceae), comparable with this study, that the absence of B-chromosomes from one population is due to the founder effect rather than to any limiting environmental factors. Bougourd and Parker (1979) presumed that B-containing plants of *Allium schoenoprasum* L. is not a response to any environmental gradient, although there are abrupt discontinuities in B frequencies at riverside populations in linear order. Different proportions of B-chromosome among populations of *S. lancifolia* does not reflect the difference in environment, but it is due to the phenomenon of the founder effect.

Table 16. Fisher's exact probability test on B-chromosome. Values are calculated by two-side test. The values under 0.05 with mark "*" or 0.01 with "**" suggest the significant difference between two samples. Symbols correspond Table 2 and 14.

	BA	BB	BC	KM	GG	PP-1	PP	GJ-1	GJ	GM	LP	BK	AS	LB
LM	.243	.304	.024*	.039*	1.11	.334	.192	.162	.251	.193	.330	.333	.806	.723
BA	–	1.60	.739	.842	.215	1.73	1.57	1.58	1.57	.011*	1.16	1.49	.092	.098
BB		–	.188	1.89	.269	1.42	1.06	1.05	1.11	.009**	1.12	1.37	.099	.113
BC			–	1.09	.030*	.044*	.131	.087	.183	.032*	.163	.432	.005**	.009**
KM				–	.045*	1.97	1.90	1.92	1.88	.001**	.242	.531	.009**	.015*
GG					–	.300	.186	.165	.229	.423	.290	.289	1.16	1.05
PP-1						–	1.58	.485	1.50	.008**	1.36	1.55	.099	.119
PP							–	1.11	1.11	.004**	.986	1.30	.051	.069
GJ-1								–	1.11	.002**	.967	1.31	.039*	.058
GJ									–	.006**	1.05	1.32	.076	.092
GM										–	.010*	.015*	.571	.903
LP											–	1.42	.110	.124
BK												–	.127	.133
AS													–	1.27

VI. Discussion and Conclusion

The species richness in tropical rain forest has been discussed elaborately, and many hypothesis have been advocated by taxonomists (Steenis, 1949, 1969, 1977), and by ecologists (summarized by MacArthur, 1972). But the basic data, analysis of genetical and biological bases of variation in a species, feature of adaptation to tropical environment, and especially biosystematical analysis of the closely related sibling species, are still imperfect. Only a few case studies had been reported on the geographical isolation or ecologically segregated distribution of plant species in tropics (Ashton, 1969; Whitmore, 1969; Burger, 1974; Morawetz, 1982). The study of the structure of local population in tropics is very few. Ehrendorfer et al. (1979) analyzed a small local population of *Drimys* in Brazil, and Sakai (1984) reported the reproductive structure of *Altingia excelsa* Noronha population in Java based on the family analysis (Sakai & Miyazaki, 1972), both species are distributed in tropics but did not belong to essential wet tropical elements.

1. Population Structure

The term population is used in wider sense in general, and usually the exactly meaning of population is determined by a prefix term such as Mendelian-, local- or species, etc. We could easily identify the individuality of *Schismatoglottis lancifolia* in Mt. Gadut area by its enormously polymorphic variations. The boundary of population or topographical distribution area and the possible occurrence area of this species is recognizable by its distinctive habitat. Nevertheless, internal population structures, such as the intermediate phase situated between each individual/clone and a local population that is limited by topographical and ecological environmental factors, are insufficiently recognized in field observations. There are so many theoretical accounts and stories on the biological species concept, but the actual population structure in the wet tropics is still obscure. Our present analysis of *S. lancifolia* torched some light on this confusing problem. The main results of the analysis of the two plots are summarized as:

1. None of the polymorphic variations correlate with gradual variations of environment factors.

2. Distribution of individuals/clones exhibits a sort of patch pattern; spatial range of size around 1 m^2 and 50–100 m^2. In the field observation, clones with plural individuals usually occupy less than 1/4 m^2.

The analysis of spatial distribution (ρ- and τ-index) in two plots certainly shows the existence of internal sub-structures. A small size clump (ca. 1 m^2 in area) may be consist of close relatives (offsprings from same parents), which is caused by the seed dispersal into limited distances around parental plants. This structure is called as micro-population. Occupied areas and the proportions of the characters are flexible in each generation.

The large size clump (up to about 100 m^2) indicates mosaic mixture of several different micro-populations each having its own characteristics. We call this

structure breeding-population, which corresponds to Wright's (1943, 1946, 1951) neighborhood size. As different neighborhoods are distributed tangly, so they can easily be cross-fertilized. Gene flow by pollen grains from one to another population is restricted within narrow area. The proportion of characters within this phase may remain somewhat constant. Inter-subplot differences at Gajabuih plot (Figs. 17, 19) and inter-site differences, such as the proportion of leaf color between Bt. Kambut and Gn. Gadut, are considered to arise from the difference of components of this phase. In the case of tropical shrub, *Drimys brasiliensis* (Winteraceae), the remarkable infra-population variation on phenotypes is maintained by allogamy, and limited pollen and seed dispersal result small effective population size (Ehrendorfer et al., 1979).

Each habitat is isolated topographically by deep dales or large streams and high mountains. Moreover, human impacts destroyed, open and rather xeric areas here and there, where individuals are to become extinct, it is impossible for invaders to establish colonies. Such places also act as isolating barriers. For example, B-chromosome component of Bt. Gambir population is extremely different from that of Bt. Gajabuih populations which is situated near Bt. Gambir, but isolated by a river (Fig. 1). Migrations to rather far distances within topographical limits may occur accidentally during a long period. This topographical limitation is called to be topo-population. Each location in this study corresponds to this phase of population.

In general geographical viewpoints induce the concept of local-population which is sometimes used for groups growing at some local limits for convenience. This category may be constructed with some topo-populations in this case.

The reproduction system and habitat leads to the hierarchical population structures, that is, individual, clone, micro-, breeding-, topo- and local-populations (Fig. 29, Table 17).

Table 17. Population structure of *Schismatoglottis lancifolia*.

Level of population	Definition	Size
Individual	Single ramete	—
Clone	Plants growing from single seed	<1 m^2
Micro-population	Parental plants and their offsprings (seed dispersal)	1-4 m^2
Breeding-population	Effective breeding population, restricted by pollinator	ca. 100 m^2
Topo-population	Population which is discontinuous by environmental or topographical factor	Various
Local-population	Populations in a paticular geographical area	Mt. Gadut area

2. Population Diversity

Now we discuss the diversity of the topo-populations. The significant differences of ratio of B-chromosome and leaf color among locations actually indicate the responsiveness of these characters to topographical isolation. On the other hand, the environmental differences is not reflected in them, but probably due to founder effect or random genetic drift. On the contrary, leaf mottle and satellite chromosome behave under

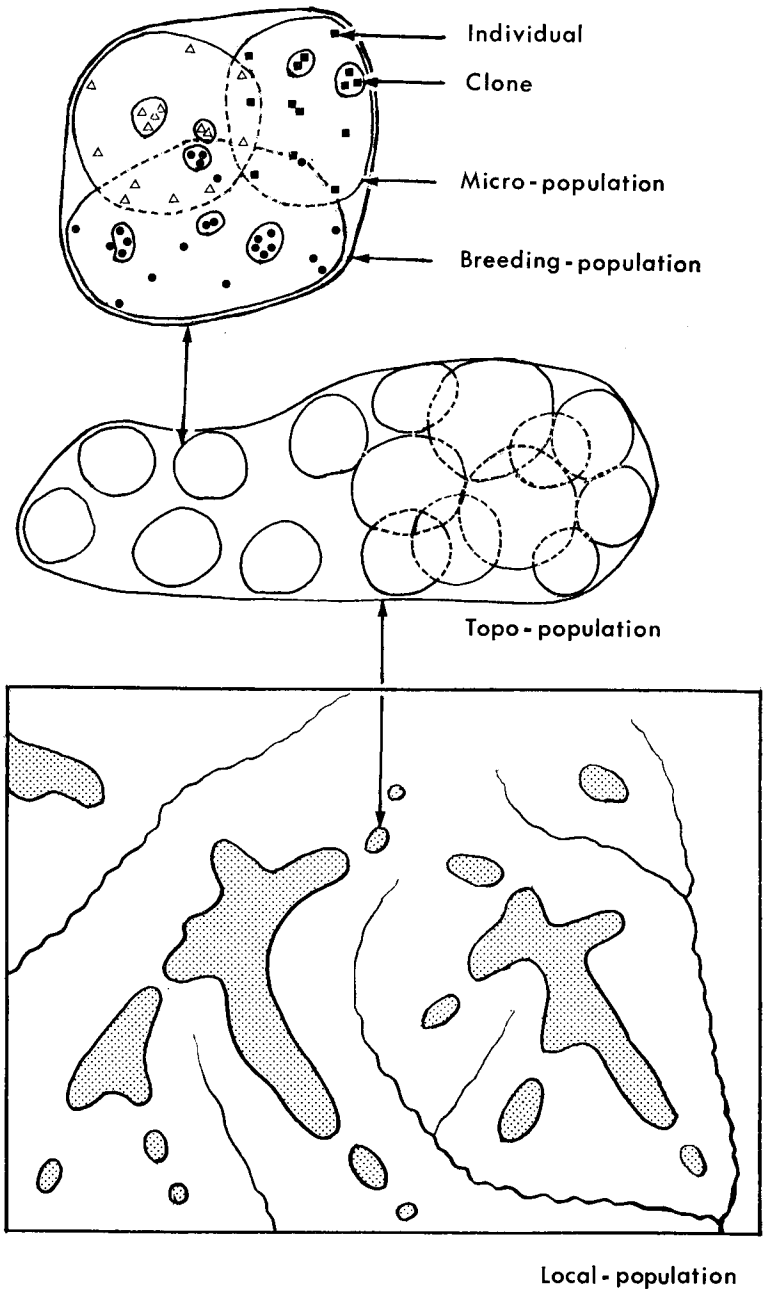


Fig. 29. Schematic illustration of population structure of *Schismatoglottis lancifolia* in Mt. Gadut area. Explanation in text.

different rules. Both populations of Gajabuih and Pinang Pinang plots seem to be completely isolated from each other by the river and by wide plantations but are situated under the similar environmental conditions. These barriers as inhibitor of reciprocal

and/or one directional migration may act stronger than the cases of the differences of B-chromosome proportion between Bt. Gajabuih and Bt. Gambir, and that of leaf color proportion between Bt. Kambut and Gn. Gadut. Nevertheless, populations of Gajabuih and Pinang Pinang plots show the same proportions of leaf mottle and satellite chromosome. Almost all populations observed show similar tendency concerning both characters (Figs. 27, 28, 30). Both proportions seem to associate with environmental conditions.

The environment seems to range from favorably to severe such as the gradient growth density in Gajabuih plot and altitudinal range from ca. 300 to 1100 meters at Gn. Gadut serial ridge. Some instances in temperate zones indicate a clear-cut connection between the polymorphisms and such environmental gradient. The distribution of *Trillium ovatum* in Pacific coast and Rocky Mountain region of western North America is one of the cases of the interaction between polymorphism and environmental variation (Fukuda & Channell, 1975). Populations of coastal region show partly homogeneity under stable habitat, and B-E chromosomes exhibit a tendency toward clinal variation in a north-south direction. Rocky Mountain populations, on the other hand, have high heterogeneity which reflects various and fluctuating climatological habitat. While, the geographical zonation of cytodemes of *Brachycome lineariloba* (Asteraceae) (2n=4, 8, 10, 12 and 16), distributed in Australia, is positively correlated with environmental gradient, i.e. the aridity (Kyhos et al., 1977). On the other hand, *Anemone Hepatica* (Ranunculaceae), with huge variations in both karyotype and phenotype, exhibits population variability different from the above cases (Mabuchi, 1980). It is concluded that no population has any correlation with the environmental gradient. Another example of a such case is found in *Liatris cylindracea* (Schaal, 1975). She found many polymorphism in allozyme, however, could not find a correlation with edaphic factors.

In the case of this study almost all populations contain surprising heterogeneity in both leaf characters and chromosomes similar to *T. ovatum*. However, proportions of no character show any association with environmental gradient in the two plots (Table 6). Further, both characters, leaf mottle and satellite chromosome, appear in certain and constant ratios with similar variants at any habitat. The examples are the populations at the serial ridges of Gn. Gadut, such as Bali Bukit (ca. 500 m alt.), Bt. Batu Bajolang (ca. 550 m), Bt. Lantik (ca. 600 m), Bt. Kambut (ca. 800–900 m) and Gn. Gadut (ca. 1100 m) locations (Fig. 26). All of the populations do not show clinal variation, but show heterogeneity as well as the relation between environmental gradient and chromosome component like those of Gajabuih plot.

Here it is clear that both proportions of leaf mottle and satellite chromosome respond neither to topographical isolations nor to environmental differences. It is a puzzling question why the variation ranges of both characters exhibit similar tendency in all populations under different and/or isolated environment?

Many models were proposed to explain the aspects of genetic polymorphism within plant populations (Hedrich et al., 1976; Ennos, 1983). These models are generally classified into two categories; the neutral or non-selection model, and balancing

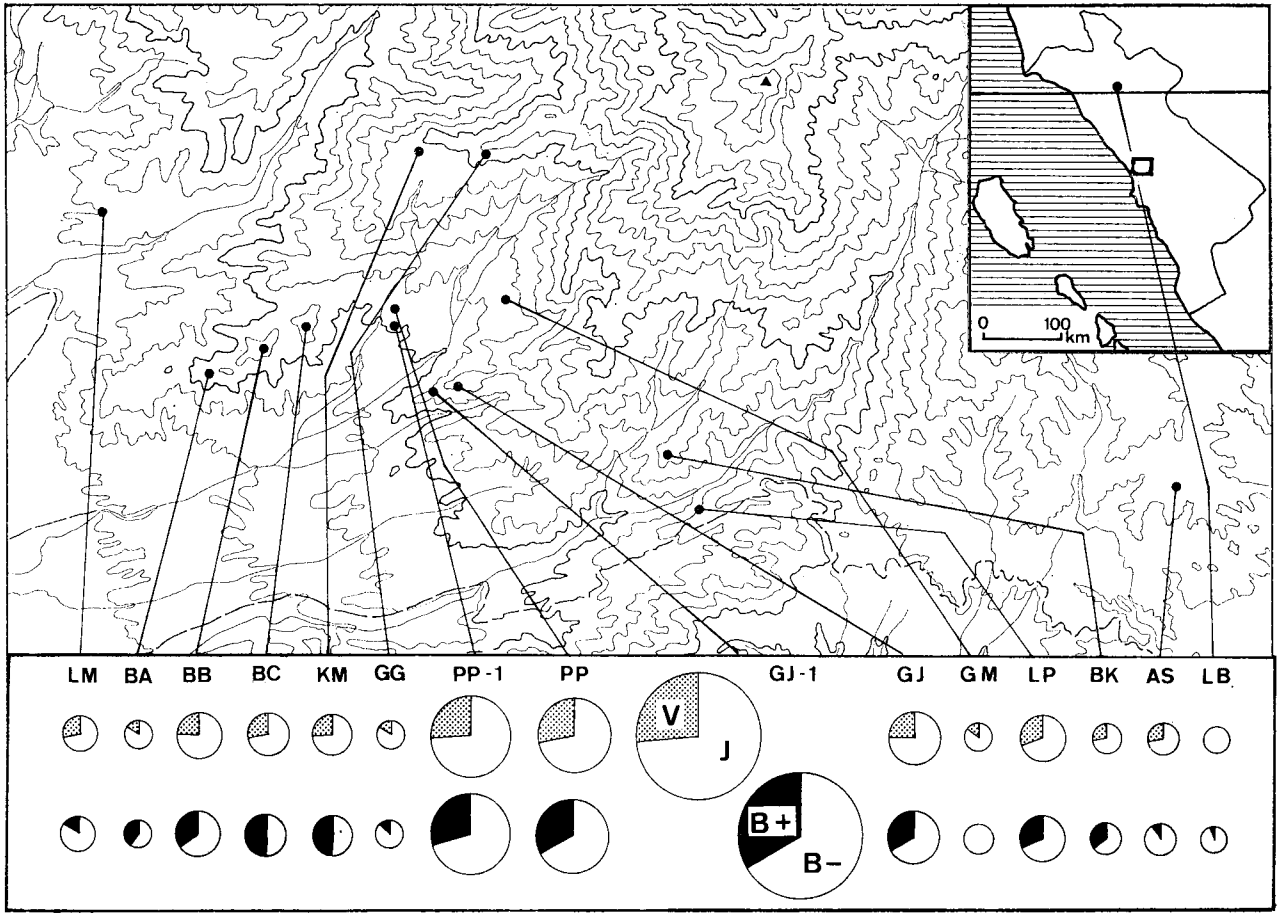


Fig. 30. The proportions of J and V types and of B-chromosomes at locations. Each size of circle diagram corresponds to each sample size. Above; satellite chromosomes. Open solid, J type; dotted, V type. Below; B-chromosomes. Open solids, without B-chromosome; black, with B-chromosome. (cf. Table 12, 14)

selection model. If the tropical rain forest is a very mild environment for this species, no selection pressure is effective. The proportion of polymorphic characters in population which are not regulated by any selection pressure happens to change by chance like that of leaf color and B-chromosome. However, it cannot be generalized to all cases. As mentioned above, population extensions are restricted by the dales, streams and mountains. Habitat segregation among allied species appears clearly at the Pinang Pinang Atas Transect plot. Hence, some selection pressure must be regulating the behavior of this species.

The main examples of balancing model are as follows:

1) Heterozygous advantage: It is considered that heterosis is one of the most efficient system maintaining genetic polymorphism to the plants with outcross pollination system like this species. Inbreeding depression which seems to be caused by homozygotic condition of several alleles is known in tropical plants (Hedrick et al., 1976). In the present case this idea is negligible as indicated by chi square test on the correlation between homo- vs. heterogeneous sets of satellite chromosome and environmental gradient of Gajabuih plot. Subplots with few individuals are presumed to be situated under rather severe environment. The heterogeneous individuals are not dominant significantly, but are distributed evenly in all subplots like the homogeneous ones.

2) Frequency dependent selection: In the case of minority superiority, the ratio of two alleles keep constant value. However, it is usually caused by the competition for limiting resource and there are few such cases in higher plant. In the present case it is difficult to consider that the leaf mottle or satellite chromosome is regulated by the effect of frequency dependent selection.

3) Diversifying selection: If the fitness of each allele changes by environmental factors, the polymorphism is maintained in the population. The environmental factor should be considered in spatial and temporal sense. In the spatial heterogeneity of environment, there are no correlation between environmental gradient and ratio of each phenotype in the case of quadrat size of 10×10 m^2. In the temporal change of environment, the condition on forest floor seems rather constant. Moreover, light intensity, which is expressed by the tree species of secondary forest element, has no clear correlation with the ratio of each phenotype (Table 6).

Besides the above mentioned facts, another reason for the preservation of polymorphism could be thought, that is the rare accidental dispersal to long distance that might occur in long period of time. Dobzhansky et al. (1977) claimed that constant migration, even of a few individuals, easily overcomes the effects of the genetic drift. Some migration from one population to others might happen. The differences in the proportion of B-chromosome and leaf color, however, suggest that seeds and pollen grains may have very few opportunities to get dispersed to other populations, passing through such barriers as deep dales or montane zone. The probability of the occurrence of migration in all populations is doubtful. The possibility of the existence of unknown differences of productivity among mutations, such as rate of flower formation, ovule and pollen grain number, kind and amount of substances attracting pollinators

and so on, can not yet be examined.

All the models mentioned above can not be explained perfectly but it can be concluded that all the polymorphism can not be explained by a single model. The variation patterns of each polymorphic character among populations is not the same. It is possible to explain that some of them, for example, leaf color or B-chromosome, have no meaning for the fitness of plants, and the difference among locations are caused by random drift or founder effect. On the other hand, the variation patterns of the leaf mottle and satellite chromosome can not be explained by the same hypothesis. It is considered that some selection mechanism is desirable for the maintenance of these variation patterns. For further explication of these mechanisms, further studies on various biological aspects of this species and related species are necessary.

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PLATE I. *Schismatoglottis lancifolia.*

A. All individuals of a small (10 m^2) area showing polymorphic variation of leaf characteristics. From left to right: plants with red petiole, red leaf beneath and green leaf surface (RRG, 6 individuals); red petiole, red beneath and white spotted surface (RRW1, 2 individuals); red petiole, green beneath and white spotted surface (RGW2, one individudal); red petiole and green leaf lamina (RGG, 2 individuals); totally green leaf (GGG, one individual). Aug. 1981, at Pinang Pinang, Ulu Gadut (subpopulation of PP-4).

B. A small colony formed by a plural clone. Four individuals possess same leaf characteristics (RGW3). Jan. 1983, Bt. Batu Bajolang, Ulu Gadut (subpopulation of BB-1).

A

B